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THE
FRESHWATER GASTROPOD MOLLUSCA OF ANGOLA

By C. A. WRIGHT
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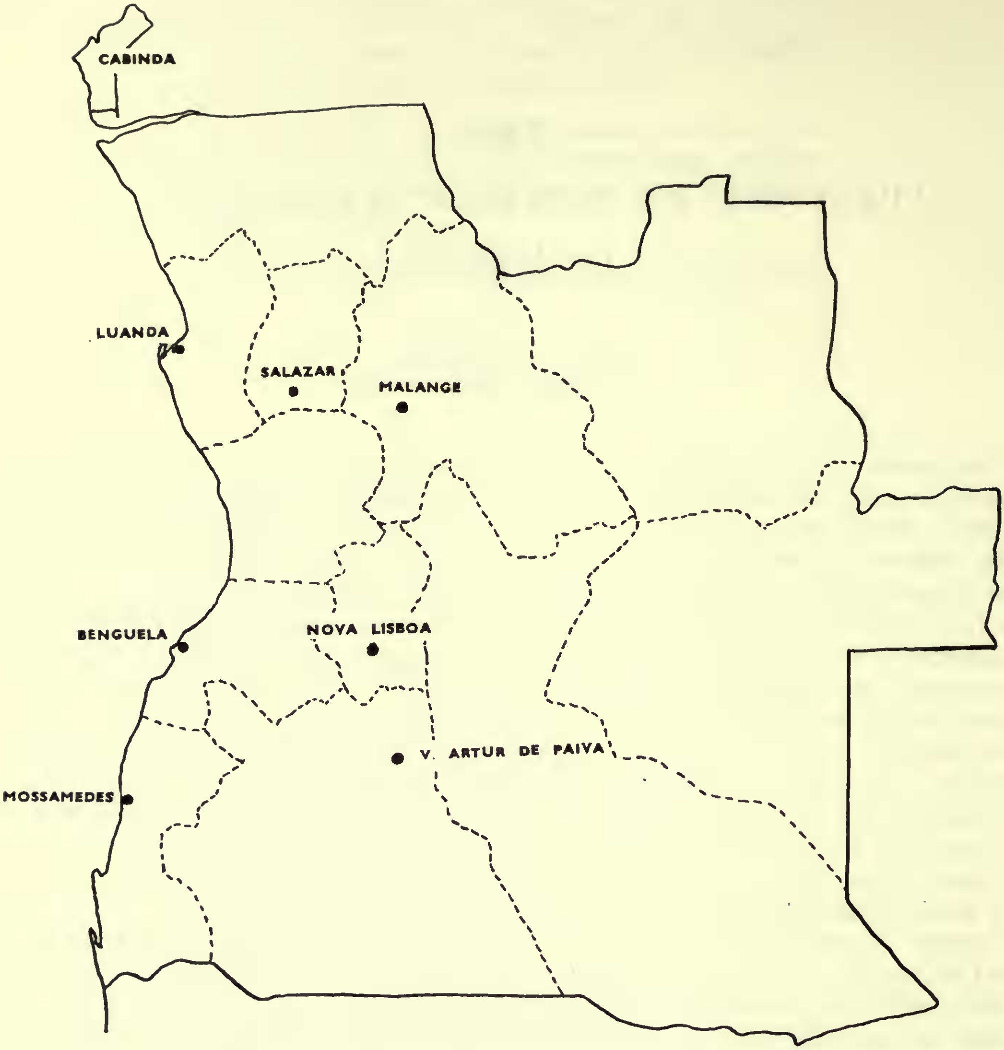
THIS account of the freshwater gastropod fauna of Angola is based largely on material collected by the author during the months of October and November 1957. Due to the enormous size of the territory and the short duration of the visit the collection cannot be considered to be completely representative of the Angolan snail fauna, but it includes the majority of species recorded from the area as well as several others not previously known to occur there. Wherever possible the type material of the species concerned has been examined and photographs of these specimens are included. Anatomical descriptions of the pulmonate species are given and an attempt has been made to indicate the range of morphological variation encountered in many of them, particularly those members of the Planorbidae which are known or potential intermediate hosts of the human blood-flukes. Synonymies are on a purely regional basis since it is felt that there is not yet sufficient information from the whole continent to justify more sweeping conclusions.

One of the primary objects of the expedition was to obtain topotype material of species described from Angola, but it became apparent that, due to inadequate definition of original localities, and to recent changes brought about by development of the country, this was not possible. The main effort was therefore concentrated on obtaining large samples of specimens from four regions of the country, the coastal plain in the neighbourhood of Luanda, the escarpment zone around Salazar, the northern part of the plateau around Malange and the southern area of the plateau in the Ganguelas district.

It is a great pleasure to acknowledge the assistance which I received from members of the Angolan Health Department, in particular the Director, Dr. Barrata Feio, also Dr. Pereira Nunes and all those who were so generous with their hospitality and time. Many other people, both private individuals and local administrators, contributed to the success of the field-collecting work and to all of them I am indebted as well as to Mr. D. Claugher who undertook the tedious work of making a great number of radula preparations.

The history of the malacological exploration of Angola covers just over a century. The first reports of shells of freshwater snails are those of Dunker (1845 and 1853) based on material collected by Dr. George Tams on a voyage to Lower Guinea in



the years 1841 and 1842. These collections were made only in the coastal region in the neighbourhood of Luanda and Benguela. In 1866 Morelet published a preliminary account of the molluscs collected by Dr. Friederich Welwitsch during his historic exploration of Angola between the years 1853–61 and in 1868 Morelet followed his earlier paper with a more comprehensive report of the malacological results of this expedition. Welwitsch's contribution to the exploration of Africa was quite outstanding ; a brief summary of the extent of his journeys is an essential part of this account, for it was the areas he visited that were the primary objectives of the present expedition. He arrived in Angola in 1854 and spent the first year exploring the coastal plain from Quizembo (north of Ambriz) to the mouth of the River Cuanza, a distance of about 120 miles. He then followed the course of the Rio Bengo inland for about 125 miles to Sange in the Golungo-Alto district and spent two years based on this centre, until ill health forced him to move up to the plateau. He travelled through Ambaca to Pungo Andongo where he set up temporary headquarters and spent eight months exploring this part of the plateau region. His journeys took him to the Cuije and Lombe rivers in the east, also to the islands of Calemba in the Rio Cuanza between the cataracts of Condo and the Quissonde rapids, a distance of about 250 miles from the coast. He visited salt marshes near Quitage and the forests on the north bank of the Cuanza, then he travelled towards the Rio Luxillo to the west of Pungo Andongo before beginning his return journey to Sange. On the way back to Sange he tried to follow the Rio Lucala up into the Duque de Braganza district but his porters deserted and he was forced to abandon this part of his journey. On his return to Luanda he made a brief trip to the Libongo area near the mouth of the Rio Lifune, then, in June 1859, he travelled by sea to Benguela, stayed for a short while in the neighbourhood of the town, and went on to Mossamedes where he stayed for about two months before exploring to the south to Pinda, Cap Negro and the Bahia dos Tigres. He returned to Mossamedes and followed the Rio Mayombo inland to Bumbo and, crossing the Serra de Xella on to the plateau of Huila, he stayed for about seven months until a tribal rebellion forced him to return to the coast and thence back to Luanda and eventually to Lisbon where he arrived in January 1861.

The collection of land and freshwater molluscs which Welwitsch accumulated during the course of these journeys was the most comprehensive ever made in Angola and was one of the major contributions to African malacology in the nineteenth century.

In 1873 Sowerby described as a new species *Physa benguellensis* and gave the type locality as Benguela, Egypt. At first sight this appears to be merely another of Sowerby's regrettable lapses of geographical accuracy but the existence of a coastal village called Egito near Benguela provides a satisfactory explanation. The next contribution to the literature on the Angolan mollusc fauna was that of von Martens (1882) with descriptions of a number of terrestrial species and a new melaniid, and some years later Nobre (1905) described the collections made by Francisco Newton in 1903.

For nearly forty years nothing further was written concerning the freshwater molluscs of Angola, but in a more general work on the bulinids of Africa Bequaert and Clench (1931) included photographs of some of the paratype specimens of species described earlier by Morelet. During this period several most important works on the fauna of neighbouring territories were published and amongst these were Pilsbry and Bequaert's (1927) exhaustive monograph on the freshwater molluscs of the Belgian Congo and Connolly's (1930) paper on the non-marine Mollusca of South-west Africa. Both of these works helped to bring the existing knowledge of the Angolan fauna into perspective with that of the rest of Africa.

Interest in African freshwater snails received a considerable stimulus from Leiper's (1915) demonstration of the part played by certain members of the Planorbidae as intermediate hosts for human blood flukes of the genus *Schistosoma*, but it was not until 1942 that this influence became active in Angola with Bruno de

Mesquita's account of schistosomiasis in the territory and his publication of a list, compiled by Germain, of possible snail hosts for the parasites. Mesquita published another paper in 1953 and Sarmento wrote on a number of foci of schistosomiasis in the south in 1944, but neither of these contributed much to the knowledge of the molluscs. In 1951 the Endemic Diseases Mission started a survey of the freshwater snails of Angola and this has resulted in several recent papers such as Azevedo and Medeiros (1956) on the anatomy of an Angolan *Biomphalaria*, Janz and Carvalho's (1956) general account of schistosomiasis in Angola with lists of mollusc species collected and, most recently, Carvalho and Janz (1960) on the Angolan species of *Bulinus*.

The province of Cabinda, although administratively a part of Angola, is separated from the rest of the territory by the Congo river and a narrow strip of the Congo Republic. It was not visited during this expedition and little is known of its mollusc fauna apart from some information in Pilsbry and Bequaert (loc. cit.) and Dartevelle's 1934 work on the aquatic molluscs of the principal river, the Shilloango.

Biomphalaria salinarum (Morelet)

Planorbis salinarum Morelet, 1868: p. 85, pl. 5, fig. 4.

MATERIAL. *Quissol* (2), Quastimbala stream, near Malange. 13 specimens 23rd October, 1957.

HABITAT. On aquatic vegetation in a very gently flowing part of a partially dammed stream.

SHELL (Pl. 1, figs. 7, 8). All of the specimens collected were immature, the largest had about 3½ whorls. The mean dimensions of the sample and the range (in millimetres) is maximum diameter 7·35 (3·5–9·8), umbilicus 2·35 (·88–3·32) and height 3·28 (2·45–4·37). The upper side of the whorls is slightly flattened and the lower side gently rounded without any well marked angulation. The first whorl on the upper side is deeply sunken and the umbilicus is shallow. The shells are white beneath the encrusting algae and detritus and a fine spiral microsculpture intersects the growth lines to give a granular appearance to the first 2½–3 whorls on the under side and, although this is present on the upper side it is not so well marked.

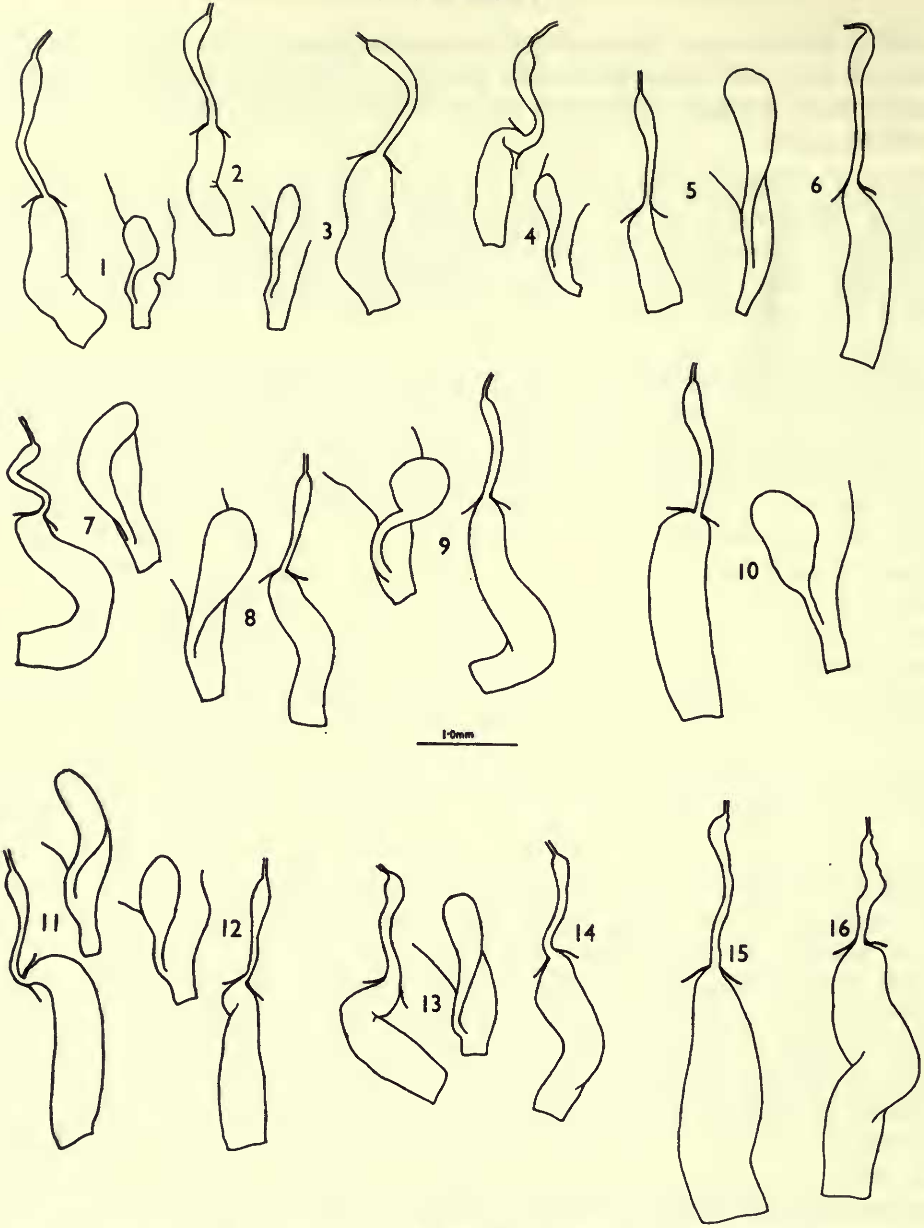
ANATOMY. The mantle varies in colour from creamy-white to pale grey with discrete black spots of fairly regular outline. The intermediate ridge between the kidney and rectum is well developed. The male copulatory organ is well developed in the specimens examined and the penis-sheath is approximately equal in length (occasionally a little longer) to the preputium and the penis is roughly as long as the sheath (Text-figs. 1–3). The prostatic diverticula are short and close-packed, most are divided but few have tertiary branches. The seminal vesicle consists of an upper part of complicated digitate diverticula from the hermaphrodite duct and a lower portion of more regular rounded protuberances. The female reproductive system is not fully developed in this material ; the receptaculum is clavate and roughly equal in length to its duct which is in turn a little longer than the vagina (Text-figs. 2, 3).

RADULA. There are about 23 teeth in each half-row of which 6–8 are tricuspid laterals. Subdivision of the endocone may occur in the fourth or fifth lateral. The endo- and mesocones of the first laterals are about equal in length, they are broad and partly fused at their bases and the tip of the mesocone is bluntly arrow-head shaped (Text-fig. 17). The ectocones of the marginals are irregularly sub-divided into several cusps of unequal size.

Biomphalaria salinarum was described by Morelet from material collected by Welwitsch from a stream near Dungo near the Rio Cuije. There is no village of this name in the area today and it was not possible to find the exact type locality but the Quastimbala stream is a tributory of the Rio Cuije and the material described here is therefore from the original district. The juvenile specimens collected do not resemble the type series (Pl. 1, figs. 1–6) closely because of the differential changes in shell form which occur with growth. However, if the ratios of shell diameter to umbilical diameter and shell diameter to height are plotted and the graphs extrapolated, the measurements for the type specimens fall close to the appropriate lines. The dimensions in millimetres of the type series are:—maximum diameter 16·3, 14·0 and 13·8; umbilicus 6·65, 5·6 and 5·4; height 4·8, 4·7 and 4·2.

The affinities of *B. salinarum* appear to be closer to the *alexandrina* species group defined by Mandahl-Barth (1957a) than to any other. The intersection of the graphs of the ratios mentioned above occurs at a shell diameter of about 13 mm. which is close to that shown by Mandahl-Barth for *B. alexandrina* and the number of whorls in the 14·0–16·3 mm. shell diameter group supports this. The broadly arrow-head shaped mesocones of the first lateral radula teeth and the subdivided ectocones of the marginals are also characteristic of the *alexandrina* group. The proportions of the male copulatory organ do not agree with those defined by Mandahl-Barth for this group in that the penis-sheath and preputium are roughly equal in length. However, Mandahl-Barth remarks that there may be differential growth of these structures and he reports immature specimens of *alexandrina* with copulatory organs resembling that of *B. rueppelli* and Abdel-Malek (1959) shows that the penis sheath in *B. boissyi* (= *alexandrina*) from Egypt is only a little longer than the preputium.

Bequaert and Clench (1933) report a series of full-grown specimens of *B. salinarum* from the Bizamba river at Boko, a tributary of the Inkisi river in the Belgian Congo and Mandahl-Barth (1957a) mentions a large, flat form of *B. pfeifferi bridouxiana* which is common in streams and rivers to the west of Katanga. Mandahl-Barth believes that this form may be *B. salinarum* but the dimensions which he quotes show that at a shell diameter of 16·5 mm. the width of the umbilicus is only a little greater than the shell height while in the type series of *salinarum* at roughly the same diameter the shell height is only about three-quarters of the umbilical width.



Figs. 1–3. *Biomphalaria salinarum*, 1 & 3 male copulatory organs and receptacula; 2, male copulatory organ. Figs. 4–6. *Biomphalaria* sp. from Senga,; 4 & 6, male copulatory organs and receptacula; 5, male copulatory organ. Figs. 7–14. *Biomphalaria pfeifferi*, 7–9, male copulatory organs and receptacula of specimens from Vila Artur de Paiva ; 10, male copulatory organ and receptaculum of specimen from Cativa ; 11 & 12, male copulatory organs and receptacula of specimens from the Rio Cului ; 13, male copulatory organ and receptaculum of specimen from Dongo; 14, male copulatory organ of specimen from Quesso. Figs. 15 & 16. *Biomphalaria* sp. from Nova Lisboa, male copulatory organs.

Biomphalaria pfeifferi (Krauss)

Planorbis pfeifferi Krauss, 1848: p. 83, pl. 5, fig. 7.
Biomphalaria adowensis; Azevedo & Medeiros, 1956.

MATERIAL

Cangombe, Huila Province. Pools in stream bed. 10 specimens, 21st November, 1957.

Cativa, Huila Province. Washing place in Rio Cuando, 7 specimens, 23rd November, 1957.

Cului (Rio), Huila Province. Bridge on Vila Artur de Paiva-Dongo road. 4 specimens. 23rd November, 1927.

Dongo, Huila Province. Pools on margin of Rio Cubangue. 3 specimens. 23rd November, 1957.

Quesso, Huila Province. Irrigation system of Granja Administrativa. 3 specimens. 21st November, 1957.

Vila Artur de Paiva, Huila Province. 17 specimens. 21st November, 1957.

HABITAT. All of the localities from which this species was collected were either in gently flowing water or in places where the water must flow during the rainy season. The snails were always found on vegetation.

SHELL (Pl. 2, figs. 3–19). Many of the specimens collected were immature with three or less whorls, the largest were those from Cangombe. The mean dimensions in millimetres of the three larger samples are :—

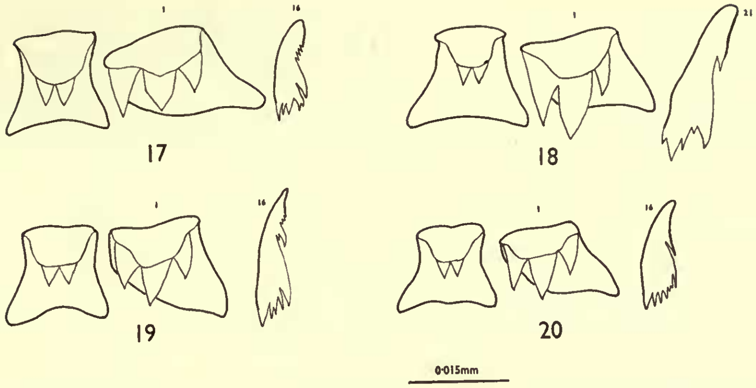
	Maximum Diameter	Umbilicus	Height
Cangombe	8·95 (6·3–13·5)	3·2 (2·45–4·72)	4·3 (3·15–6·82)
Cativa	7·05 (4·2–9·8)	2·25 (1·05–3·32)	3·43 (2·97–4·2)
Vila Artur de Paiva .	7·95 (3·67–10·0)	2·97 (1·22–4·02)	3·51 (2·8–3·85)

These measurements show that the shells are relatively high for their diameters (except those from Vila Artur de Paiva), and are more widely umbilicate than is usual in this species. The diameter of the whorls increases relatively rapidly and the first whorls on the upper surface are more deeply sunk than the umbilicus ; they are gently rounded on the upper surface and there is a very blunt angle near the suture on the underside. The shells are pale yellowish-brown and translucent. All have a delicate spiral sculpture which intersects the growth lines to give a fine but well-marked granular appearance under high magnifications. In the specimens from Cangombe, Cativa, the Rio Cului and Vila Artur de Paiva this micro-sculpture is well developed on all whorls on both sides but in the samples from Dongo and Quesso it is better developed on the underside than on the top.

ANATOMY. The ground colour of the mantle is light grey and it is marked with spots and blotches of black of fairly regular outline. In larger individuals the right side of the mantle is more intensely pigmented than the left. The intermediate mantle ridge is well developed. The proportions of the male copulatory organ are rather variable (Text-figs. 7–14). The majority of specimens have the penis-sheath a little shorter than the preputium but in some of the smaller specimens the sheath is only about two-thirds or half the length of the preputium. The penis is roughly equal in length to the sheath but in a few individuals it is slightly longer and extends into the preputium. The seminal vesicle in most individuals has a complicated system of digitate diverticula similar to the upper part of the vesicle in *B. salinarum.* The receptaculum seminis is so variable in shape according to the maturity of the individual specimens that it can have little taxonomic significance (Text-figs. 7–13). In general it is pyriform and the dilated part is about half as long again as the duct.

RADULA. The number of teeth in each half-row varies between 19 and 25, and there are 6–8 tricuspid laterals on each side of the central. These figures do not appear to vary much with the size of the individual. There are some differences in the characters of the cusps of the laterals, in the majority of specimens the mesocone of the first laterals is triangular (Text-fig. 19) but in some it is slightly arrow-head shaped. Most of the individuals have the endo- and mesocone of the first laterals roughly equal in length but two specimens (one from Cangombe and one from Quesso) have the mesocone distinctly longer while in two others (Dongo and Quesso) the endocone is the larger cusp. One of the specimens from the Rio Cului had the cusps of the first laterals distinctly broader and shorter than in any of the other specimens. The ectocone of the marginals is sometimes single and sometimes subdivided, but this is a character which varies considerably in the same radula and the undivided condition seems to be the commonest.

Biomphalaria pfeifferi is a widespread and variable species which has so far not been recorded with certainty in Angola. Azevedo and Medeiros (1956) described the anatomy of a species which they called *B. adowensis* from Bailundo near Nova Lisboa in Huambo Province and considered that this form was different from *B. pfeifferi* from Mocambique. However, Schutte and van Eeden (1959) suggest that *B. adowensis* cannot be regarded as distinct from *B. pfeifferi* and Mandahl-Barth (1957a) considers that it is doubtful if *B. adowensis* and *B. pfeifferi rueppelli* (Dunker), are different. In the same paper Mandahl-Barth mentions the occurrence of a small species of *Biomphalaria* from the Chibia district (Huila Province) of Angola in which the shell resembles that of typical *pfeifferi* but in which the anatomical characters are closer to those of *B. p. rueppelli.* More recently Mandahl-Barth (1960) has suggested that all of the forms which he had earlier regarded as subspecies of *B. pfeifferi* (with the exception of *B. rhodesiensis*) should no longer be considered distinct but should be regarded as variants of a single species. The description given by Azevedo and Medeiros (1956) might well apply to some of the specimens examined in this work and there is no doubt that the proportions of the male copulatory organ described here are closer to those of *rueppelli* from Ethiopia (Wright and Brown, 1962) than they are to those of *pfeifferi* from South Africa (Schutte and van Eeden, 1960). Similarly, the shape of the lateral radula teeth is more like that of *rueppelli* than that of *pfeifferi* but the subdivision of the ectocone of the marginals is extremely irregular and in this respect agrees both with Schutte and van Eeden's (1959) observations in *pfeifferi* and Wright and Brown's (1962) finding in *rueppelli.* Until a much more extensive study of the African members of *Biomphalaria* has been carried out it is not possible to be certain of the affinities of any particular group of populations.



FIGS. 17–20. Radula teeth of *Biomphalaria*. Fig. 17. *Biomphalaria salinarum*. Fig. 18. *Biomphalaria* sp. from Nova Lisboa. Fig. 19. *Biomphalaria pfeifferi*. Fig. 20. *Biomphalaria* sp. from Senga.

Biomphalaria sp. (1)

MATERIAL. *Senga, Huila Province*, stream near village, 5 specimens, 22nd November, 1957.

HABITAT. The snails were found on aquatic vegetation in gently flowing water.

SHELL (Pl. 1, figs. 9, 10). The shells are more depressed and more broadly umbilicate than those of *B. pfeifferi* and the whorls do not increase in size so rapidly, they are almost flattened on top and slightly carinate beneath on at least the first three whorls. There is a well-marked spiral micro-sculpture on the underside extending well on to the third whorl. The three largest specimens (all just under four whorls) are about 8 mm. diameter, 2·8 mm. high and have an umbilical diameter of about 2·8 mm. The colour is light reddish-brown and the growth lines are irregular giving a rather rugose appearance.

ANATOMY. Three of the five specimens were dissected. The characters of the mantle are in no way remarkable. The male copulatory organ is a little longer and more slender than in *B. pfeifferi* and the sheath is either longer than or at least equal to the preputium in length (Text-figs. 4–6). The prostate is longer and the diverticula are less closely packed than in *B. pfeifferi*. The vesicula seminalis has only smoothly ovoid protuberances and is thus similar to the lower part of the vesicle in *B. salinarum*. The receptaculum seminis is clavate and the dilated part is about equal in length to the duct (Text-figs. 4, 6).

RADULA. There are 18–24 teeth in each half-row of which 7 or 8 are tricuspid laterals. The mesocones of the laterals are triangular and the endocones of at least the first laterals are as long or longer than the mesocones and they are sharply pointed. The majority of the marginal ectocones are undivided (Text-fig. 20).

No attempt has been made to allocate this material to any known species because there are not enough specimens for a sufficiently detailed description to be made. Apart from their small size the shells show a similarity to those of the *alexandrina* group in their general form. The proportions of the male copulatory organ are more similar to those of the *sudanica* group and the characters of the radula would certainly not preclude the inclusion of these specimens in that group. It is possible that this sample represents a slightly aberrant form of *B. rhodesiensis* but speculation on its affinities is not likely to be constructive. The point of interest is that the sample comes from an area in which *B. pfeifferi* is generally distributed and there is no doubt that this form differs from that which is locally dominant.

Biomphalaria sp. (2)

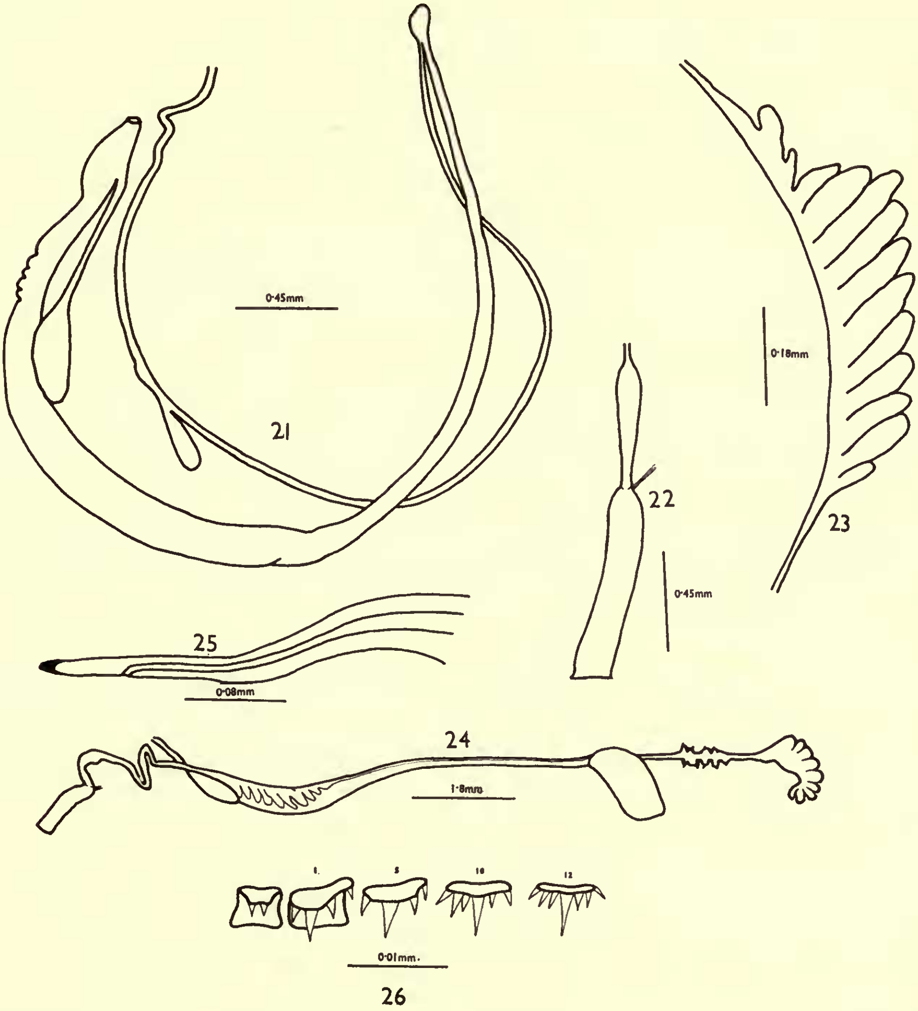
MATERIAL. *Nova Lisboa, Huambo Province.* Sample provided by Dr. Morais de Carvalho, no further details available. 23 specimens.

SHELL (Pl. 2, figs. 1, 2). The sample is fairly uniform in size, the mean dimensions and range in millimetres being, diameter 13·7 (12·7–14·9), height 5·1 (4·55–6·1) and umbilical diameter 4·9 (4·7–5·25). The shells are higher than those of *B. salinarum* and the whorls are more rounded, showing no carination. The fine spiral microsculpture extends well on to the third whorl on the underside but is more restricted on the upper surface. The colour of the shells is light brown.

ANATOMY. Unfortunately none of the specimens was sufficiently well preserved to allow a full study of the anatomy. The male copulatory organ is large and the penis-sheath is about half as long as the preputium (Text-figs. 15, 16). The penis extends just into the preputium and its tip is often bent but this may be a fixation artefact.

RADULA. The radula differs from those of all of the other *Biomphalaria* examined in this work by the long dagger-like mesocones of the lateral teeth being united at the base with the sharply pointed endocones of nearly equal length and by the ectocones being much shorter. There are 25–28 teeth in each half-row, of which 13–15 are tricuspid laterals. The ectocones of the marginals are undivided, almost without exception (Text-fig. 18).

The affinities of this form are not readily determined. If the ratios of umbilical diameter to shell diameter and height to shell diameter are plotted a random distribution of the points is obtained around the mean shell diameter of 13–14 mm., suggesting an intersection of the lines for these two ratios at about this size. This character suggests a relationship to the *alexandrina* group, but the proportions of the male organ (which may be unreliable due to poor fixation) are more like those for the *pfeifferi* group. The form of the radula is unlike that of any of the others examined in this study but it has possible affinities with the *alexandrina* group. More material from the central plateau region must be studied in great detail before conclusions about the relationships of this form can be made, but it is possible that it may have affinities with the large, flat form of *B. pfeifferi bridouxiana* described by Mandahl-Barth (1957a) from rivers in the Congo and mentioned in the discussion of *B. salinarum.*



Figs. 21–26. *Anisus misellus.* Fig. 21. Part of genital system showing uterine glands, receptaculum and aberrant prostate consisting of a single diverticulum. Fig. 22. Male copulatory organ. Fig. 23. Normal prostate. Fig. 24. Whole genital system. Fig. 25. Tip of penis showing cap-like cuticular stylet and sub-terminal opening of vas deferens. Fig. 26. Radula teeth.

Anisus misellus (Morelet)

Planorbis misellus Morelet, 1868: p. 85, pl. 5, fig. 5.

MATERIAL

Panguila (*Lagoa*), lake near mouth of the Rio Bengo. 36 specimens. 8th November, 1957.

Quifangondo, marsh on the bank of the Rio Bengo. 12 specimens. 16th November, 1957.

Lalama (*Lagoa*), lake near junction of Rio Calucala and Rio Bengo. 11 specimens. 14th November, 1957.

Bom Jesus, small lake on bank of Rio Cuanza. 4 specimens. 13th November, 1957.

Dondo, Rio Mucoso (included in sample of *B. forskali* received from Dr. Morais de Carvalho). 3 specimens. 3rd July, 1957.

Quionqua (2), small pool beside road. 9 specimens. 24th October, 1957.

HABITAT. This species was found in habitats ranging from a small stagnant pool to pools in a floating marsh and on aquatic plants in large lakes but not (with the possible exception of the material from Dondo whose habitat is not known) in flowing water.

SHELL (Pl. 3, figs. 25, 26). Small, flattened, largest specimens with 4–4½ whorls which increase slowly in size and scarcely overlap one another. The shells are almost completely flattened beneath and slightly concave above but in some individuals this may be reversed. The lower edge of the periphery is bluntly angulate, the aperture is sometimes slightly raised and the sutures are shallow. The colour varies from reddish- to pale yellowish-brown and the sculpture consists of fine growth lines and an irregular punctation with fine spiral lines which are particularly well marked on the underside. The largest specimens seen are about 5 mm. diameter and 1·2 mm. high.

ANATOMY. The mantle is very light grey, almost white, with sparse grey markings and a grey-blue border. The pseudobranch consists of two relatively large flaps attached to the anal lobe. The male copulatory organ is slender, the penis sheath is narrow, slightly dilated proximally and about half the length of the preputium which is roughly twice as wide as the sheath (Text-fig. 22). The penis is a little longer than the sheath and is tipped with a very small, cap-like cuticular stylet (Text-fig. 25), the opening of the vas deferens is subterminal. The vas deferens is not exceptionally long and the prostate, consisting of about a dozen simple diverticula, is closely applied to the uterus (Text-fig. 23). Several of the specimens which were examined had only a single large prostatic diverticulum (Text-fig 21). The sperm duct is long and straight and the convolutions of the seminal vesicle on the hermaphrodite duct have numbers of small protuberances. The vagina is short and dilated into an ovoid vaginal bulb into which opens the long duct of the receptaculum seminis (Text-fig. 21). The receptaculum is ovoid and about half the length of its duct. The uterus is long and narrow and has a series of corrugations near to its junction with the vagina but it is otherwise straight and grades almost imperceptibly into the straight oviduct. The albumen gland is relatively small (Text-fig. 24).

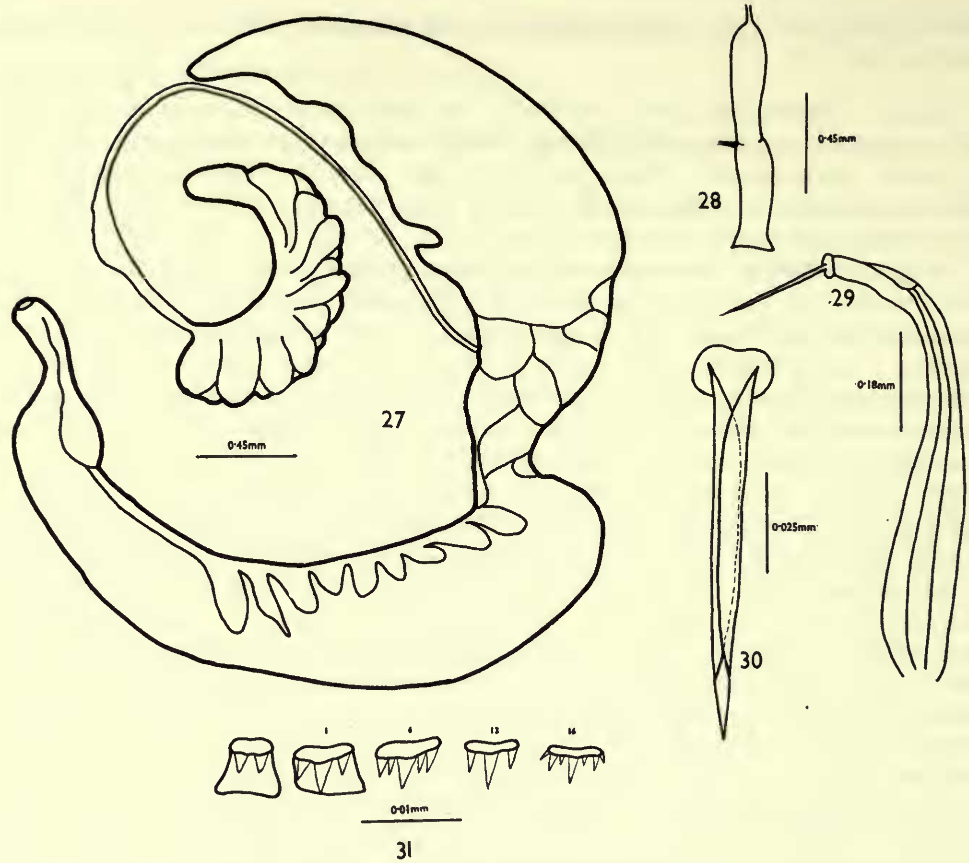
RADULA. The radula teeth are small, the centrals are bicuspid and the first five laterals are basically tricuspid but usually with a very small fourth cusp high up outside the ectocone. There are about eight marginal teeth in each half row and these are six- or seven-cusped, with a large narrowly pointed mesocone and smaller lanceolate cusps on either side of it (Text-fig. 26).

The type locality for *A. misellus* is the Lagoa Quilunda from which no specimens were obtained during this investigation. However, Lagoa Lalama is a short distance up-stream on the Rio Bengo from Quilunda and Lagoa Panguila and the marsh at Quifangondo are a few miles down-stream on the same river so that some of the material described here is from very close to the type locality. The present specimens compare well with those in the type series although the punctate pattern is not easy to make out on the original material (Pl. 3., figs. 19–24).

This species has been generally regarded as synonymous with *A. natalensis* (Krauss) but the anatomy of *natalensis* has recently been described (Wright and Brown, 1962) and the structure of the male copulatory organ in the two species is quite different, also the punctate shell sculpture on *misellus* does not appear to have been reported on *natalensis*. In *natalensis* the terminal part of the penis is sclerotised progressively towards the tip and the vas deferens opens almost terminally with a group of backwardly directed spines surrounding its aperture, while in *misellus* the penis-tip bears a minute but distinct cap-like stylet and the vas deferens opens well back from the end.

Binder (1958) has described the anatomy of *Gyraulus gibbonsi* from the Ivory Coast and the structure of the penis in this species and *misellus* is very similar. The stylet in *gibbonsi* appears to be more sharply pointed and the opening of the vas deferens is closer to the penis tip, also the penis is longer, extending about half way into the preputium. According to Binder, the prostate in *gibbonsi* is a long tubular structure without diverticula, a most unusual feature in the Planorbidae, but this is possibly an extreme development of the single prostatic diverticulum found in some specimens of *misellus*. The length of the receptaculum seminis duct appears to be relatively shorter in *gibbonsi* than in *misellus* and Binder shows the vesicula seminalis to be smooth and without tubercles. The cusps of the radula teeth in *gibbonsi* are broader and less lanceolate than those in *misellus* and the mesocones of the marginals are less prominent. These differences seem to justify the retention of these two forms as separate species for the time being but Hubendick (1957) has shown that individual variation in this type of penis structure in *Anisus crista* can be considerable. One fact, however, is certain, and that is that both the Ivory Coast form and the species from Angola are distinct from *A. natalensis*.

The generic and sub-generic nomenclature in this group of small planorbids is at present very confused and must await the study of more material before it can be clarified. If the characters of the penial stylet are to be used as a basis for grouping the species then *misellus* and *gibbonsi* belong in the *crista* group (placed by Hubendick in the sub-genus *Armiger*) while *natalensis* must stand on its own.



Figs. 27–31. *Gyraulus costulatus*. Fig. 27. Whole genital system without male copulatory organ. Fig. 28. Male copulatory organ. Fig. 29. Penis showing stylet and sub-terminal opening of vas deferens. Fig. 30. Penial stylet. Fig. 31. Radula teeth.

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848: p. 83, pl. 5, fig. 8.

MATERIAL

Dongo, Rio Cubangue, Huila Province. 10 specimens. 23rd November, 1957.
Cangombe, stream, Huila Province. 6 specimens. 21st November, 1957.
Cului (*Rio*), at bridge on road from Dongo to Vila Artur de Paiva, Huila Province. 2 specimens. 23rd November, 1957.
Cativa, Rio Cuango, Huila Province. 5 specimens. 23rd November, 1957.
Gunda-Vunjanga, Huila Province. 1 specimen. 22nd November, 1957.

Moembege (*Rio*), Agricultural Research Station, Salazar. 3 specimens. 29th October, 1957.

Quissol (2), Quastimbala stream (near Malange). 2 specimens. 23rd October, 1957.

HABITAT. The only consistent feature about the six localities in which this species was found is that in all of them the water was either flowing or was a more or less static pool in a stream bed which would contain flowing water during the wet season. None of the samples was found in truly stagnant or heavily polluted water and most of the habitats had almost complete sun exposure.

SHELL (Pl. 3, figs. 27–30). 3–3½ whorls rapidly increasing in size, upper side convex, lower concave, a variable basal angle at the periphery of the outer whorl. Many of the shells are heavily coated with algae and deposits, the colour of the shell itself is whitish, it is strongly and slightly irregularly ribbed and the degree of ribbing varies somewhat between populations. No other sculpture was observed.

ANATOMY. Mantle light grey to almost white, a moderately well-developed simple pseudobranch lobe is present. The male copulatory organ is short, the proportions of the penis sheath and preputium vary slightly but they are usually about equal in length and roughly equal in width, the preputium being a little wider than the main part of the sheath (Text-fig. 28). The penis varies in length, it may extend well into the preputium or only just reach the junction between the preputium and sheath. The tip of the penis is equipped with a well-developed dagger-like stylet the base of which is discoidal and the edges of the blade are rolled over to form a channel which opens near to the tip of the stylet (Text-fig. 30). The vas deferens opens a short distance from the end of the soft part of the penis and a groove from the opening leads down to the channel in the stylet (Text-fig. 29). The vas deferens runs back to the prostate which has about nine short and rather irregular wide diverticula and is closely applied to the proximal end of the glandular uterus. The sperm duct is short and the vesicula seminalis is a simple asymetrical swelling near to the proximal end of the hermaphrodite duct. The vagina is short and slightly dilated to form a vaginal bulb, the receptaculum seminis duct opens into the bulb, the receptaculum is club-shaped and about equal in length to its duct. The oöthecal and muciparous glands surrounding the uterus are massive and the oviduct is strongly convoluted. The albumen gland is very large (Text-fig. 27).

RADULA. The radula teeth are small, the centrals are bicuspid, the first five laterals are tricuspid and the remaining twelve to fourteen teeth in each half-row show a gradual increase in the number of cusps until the extreme marginals have about seven (Text-fig. 31). The cusps are broader and less needle-like than those of *Anisus misellus* but otherwise the teeth are very similar in the two species.

G. costulatus was originally described from Natal but there are records of its occurrence in many areas in Africa and it is in no way surprising that it should also be found in Angola. The anatomy of this species has been described by Ranson (1955) and Azevedo et al. (1957), in both cases the descriptions are based on material from the Sul do Save province of Mozambique and they compare well with the present material. The close similarity in the illustrations of the two published descriptions does not give an indication of individual variation within the species.

The structure of the stylet in this species is similar to that described by Baker (1945) for several species of *Anisus* (including the genotype, *A. spirorbis*) and *Gyraulus* and it agrees in general structure but not in detail with that described by Hubendick (1958) for *Gyraulus trapezoides*.

Lentorbis benguelensis (Dunker)

Planorbis benguelensis Dunker, 1845: p. 8, pl. 2, figs. 1–4.

MATERIAL

Lalama (*Lagoa*), lake near junction of Rio Calucala and Rio Bengo. 6 specimens. 14th November, 1957.

Panguila (*Lagoa*), north-west corner of lake near the mouth of the Rio Bengo. 2 specimens. 9th November, 1957.

Quifangondo, marsh on banks of Rio Bengo. 3 specimens. 16th November, 1957.

HABITAT. The specimens from Lalama were collected together with *Segmentorbis kanisaensis* and *Anisus misellus* in the reed bed fringing the lake, those from Panguila were found with *A. misellus* and *B. forskali* on lily leaves and *Ceratophyllum* and the material from Quifangondo was taken together with *A. misellus* in small pools in a floating marsh.

SHELL (Pl. 3, figs. 15, 16). Lenticular, upper side convex, more or less flat beneath, lower angle gently curved, whorls overlapping one another, umbilicus narrow, colour pale yellowish-brown, very fine growth lines and fine spiral sculpture, most marked on the underside. Five of the Lalama specimens and two of those from Quifangondo had small internal septa, either one or two sets in the last whorl. The basal lamella in each set is relatively short, extending about half to two-thirds of the width of the whorl, the inner one curves over the inner wall and projects well into the lumen of the whorl. The outer lamella is short and more or less straight on the steepest part of the outer wall while the dorsal is a simple circular protuberance and is not always present (Text-figs. 34, 35). The dimensions of the largest specimen (from Lalama) were :—diameter, 4·9 mm., umbilicus 1·3 mm. and height 1·82 mm.

ANATOMY. All of the specimens except the two smallest from Lalama were dissected, six were aphallic and of the three with copulatory organs two were grossly infested with sporocysts of an unidentified furcocercous cercaria and the third contained many metacercarial cysts. As a result no complete genital system was obtained intact and this description is based on a composite picture derived from several individuals.

The mantle is greyish-white with darker markings along the edges of the kidney which is narrow proximally and widens toward the anterior end. No ridges were observed on the underside of the mantle. The male copulatory organ is large, the sheath is a little longer and only slightly narrower than the preputium, the maximum diameter of the proximal dilatation of the sheath is about equal to the diameter of the preputium (Text-fig. 38). The penis is long, about equal in length to the combined lengths of the sheath and preputium and it lies coiled within the sheath. The upper part of the preputium contains a large, glandular lobe in addition to the usual two muscular pillars. The vas deferens is long and convoluted, in aphallic specimens where no prostate is developed it is often present but it is narrow and straight. The prostate consists of about twelve irregularly shaped diverticula and it lies well back, closely applied to the proximal glandular part of the uterus (Text-fig. 39). The vagina is short and leads into the long uterus, the distal part of which is slightly convoluted and surrounded by a yellowish-orange oöthecal gland while the proximal part is straight and surrounded by a translucent white muciparous gland. The receptaculum seminis is small and club-shaped, the duct is about equal in length to the sac (Text-fig. 40). The vesicula seminalis is little more than a dilatation of the hermaphrodite duct and does not appear to have marked protuberances.

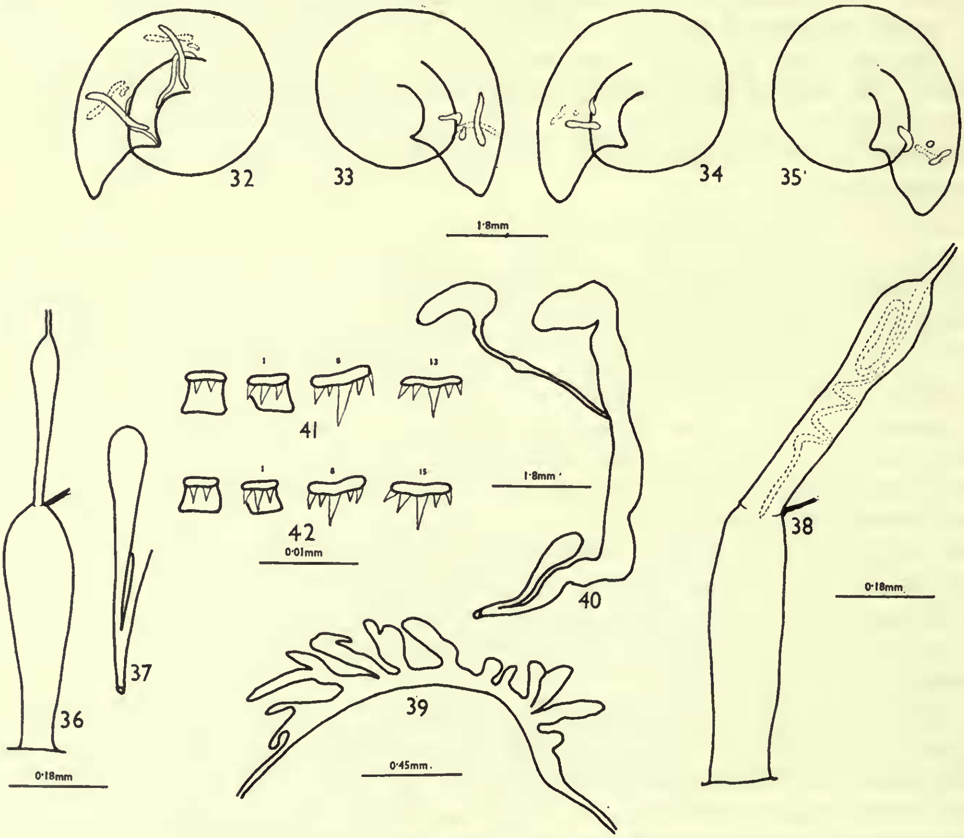
RADULA. The teeth are extremely small and it is difficult to make out their structure with accuracy. The centrals are bicuspid and the first seven teeth in each half row appear to be only tricuspid but there is a possibility of very fine interstitial cusps on either side of the mesocone. The remaining eleven teeth in the half row are at least five-cusped, the mesocone dominating (Text-fig. 42).

Planorbis benguelensis was described by Dunker from shells collected in the region of Benguela. Two of his original specimens from the Berlin Museum have been examined (Pl. 3, figs. 5–10) and the present material agrees well with them except that the original specimens are larger (6·9 and 6·0 mm. diameter) and have no trace of internal lamellae.

P. benguelensis was referred to *Hippeutis* by Pilsbry and Bequaert (1927) but in 1954 Mandahl-Barth showed that the other African species placed in *Hippeutis*, *H. junodi* Connolly, 1922, was anatomically distinct from the Palaearctic members of the genus and he created the genus *Lentorbis* for the two African species with *benguelensis* as type species.

The large proportion of specimens with internal lamellae in the present material appears to be unusual. Mozeley (1939) reported finding a species of *Hippeutis* in Tanganyika which resembled *junodi* but for the presence of a small tooth in the final whorl of some specimens, a character not mentioned by Connolly in his original description of the species or illustrated by him in the figure published later (Connolly, 1925). However, examination of the type series (Pl. 3, figs. 1–4) of *junodi* shows that four out of the seven specimens have at least one basal lamella in the body whorl.

The anatomy of *L. junodi* has been described briefly by Mandahl-Barth (1954) and more fully by Azevedo, Medeiros and Costa Faro (1957). There are several fairly clear anatomical differences between *benguelensis* and *junodi*. The male copulatory organ of *junodi* is illustrated by Azevedo et al. as having the sheath at least twice as long as and, apart from the proximal dilation, as being very much narrower than the preputium. In *benguelensis* the sheath and preputium are more nearly equal in length and diameter. The receptaculum seminis in *junodi* is very large and sac-like, extending right back to the level of the albumen gland while that in *benguelensis* is much smaller, ovoid and extends posteriorly only about half way up the length of the oöthecal gland. There are some differences also in the form of the radula teeth illustrated by Azevedo et al. and those seen in specimens of *benguelensis* but because of the minute size of the teeth and the possibility of misinterpreting their detailed structure it is perhaps best not to emphasize these differences.



Figs. 32 & 33. Shell of *Segmentorbis kanisaensis* showing internal lamellae. Fig. 32. Ventral view. Fig. 33. Dorsal view.

Figs. 34 & 35. Shell of *Lentorbis benguelensis* showing internal lamellae. Fig. 34. Ventral view. Fig. 35. Dorsal view. Fig. 36. *S. kanisaensis*, male copulatory organ. Fig. 37. *S. kanisaensis*, receptaculum. Fig. 38. *L. benguelensis*, male copulatory organ. Fig. 39. *L. benguelensis*, prostate. Fig. 40. *L. benguelensis*, whole genital system of aphallic specimen. Fig. 41. *S. kanisaensis*, radula teeth. Fig. 42. *L. benguelensis*, radula teeth.

Segmentorbis kanisaensis (Preston)

Segmentina kanisaensis Preston, 1914: p. 265, pl. 18, figs. 17–19.

MATERIAL

Lalama (*Lagoa*), lake near junction of Rio Calucala and Rio Bengo. 7 specimens. 14th November, 1957.

Quequesse (*Lagoa*), lake on Cuanza flood plain. 1 specimen. 13th November, 1957.

HABITAT. In the reed-bed fringing the lake, collected together with *Anisus misellus* and *Lentorbis benguelensis*.

SHELL (Pl. 3, figs. 17, 18). Flattened, lenticular, upper side convex, lower side almost flat, basal angle sharp forming a slight carination, whorls overlapping one another and umbilicus narrow. The shells are light yellowish or almost colourless and the sculpture consists of fine growth lines and very fine spiral lines on the under side and an extremely fine pitting on the upper surface. The aperture is slightly deflected downward. All of the shells are internally septate with two or three sets of lamellae except the smallest which has only one set. The basal lamella extends almost the whole width of the body whorl and is slightly S-shaped, the inner lamella curves downward anteriorly over the inner wall of the whorl and runs forward along the inner angle of the suture for a short distance. The outer lamella curves over the upper outer angle of the whorl and the dorsal consists of a simple comma- or lozenge-shaped protuberance (Text-figs. 32, 33). The largest specimen in the sample had a diameter of 4·2 mm., umbilicus 1·27 mm. and height 1·27 mm.

ANATOMY. Three specimens were dissected of which two proved to be aphallic. The mantle is fairly uniformly spotted with dark grey except over the kidney where the colour is lighter. The male copulatory organ is relatively large, the penis sheath is slender with a slight proximal dilatation and it is about equal in length to the preputium which is much wider (Text-fig. 36). The vas deferens is long, thin and sinuous and the prostate resembles that in *Lentorbis benguelensis*. There are no nodules on the seminal vesicle which is a simple dilatation of the hermaphrodite duct about half way along its length. The female genital system resembles that of *L. benguelensis* except for the receptaculum which is slightly club-shaped and merges gradually with its duct (Text-fig. 37).

RADULA. As in *L. benguelensis* the teeth are extremely small and no significant differences have been observed between the two species except that there are fewer in each half row in *kanisaensis* (1+5+8) than in *benguelensis* (1+7+11) (Text-fig. 41).

Mandahl-Barth (1954) separated the African species placed in *Segmentina* from the Palaearctic members of the genus and created for them the genus *Segmentorbis* with *S. angusta* Jickeli as type species. The basic anatomical difference between *Segmentina* and *Segmentorbis* is that there are two flagellae on the penis of *Segmentina* and only one in the African genus. For *S. kanisaensis* which lacks a flagellum altogether Mandahl-Barth created the sub-genus *Carinorbis* but this name was pre-occupied and in 1956 he proposed the new sub-generic name *Acutorbis*.

Originally described from the southern Sudan, *S. kanisaensis* (Pl. 3, figs. 11–14) has been reported from Uganda and Tanganyika by Mandahl-Barth (1954), from South Africa by Connolly (1939), from the Gambia by Smithers (1956) and from the Ivory Coast by Binder (1957) and thus seems to have an extremely wide distribution which is further extended by this record from Angola.

With the small amount of material which has been available for this study it is not possible to draw major conclusions as to the status of the genera *Lentorbis* and *Segmentorbis* but further work may show that the two are not clearly distinct.

Bulinus globosus (Morelet)

Physa globosa Morelet, 1866: p. 162.

Physopsis globosa Morelet, 1868: p. 93, pl. 9, fig. 4.

MATERIAL

Fazenda Tentativa, sugar plantation near the mouth of the Rio Dande. Two localities : (1) stream carrying effluent from sugar refinery, 22 specimens ; (2) irrigation ditches on the plantation, 41 specimens. 8th November, 1957.

Matoz (*Lagoa*), drainage ditch beside small lake on the edge of Fazenda Tentativa. 37 specimens. 8th November, 1957.

Libongo (*Fazenda*), irrigation ditches on oil palm plantation near mouth of Rio Lifune. 12 specimens. 9th November, 1957.

Quilunda (*Lagoa*), large lake on the banks of the Rio Bengo. 35 specimens. 14th November, 1957.

Lalama (*Lagoa*), lake near junction of Rio Calucala and Rio Bengo. 7 specimens. 14th November, 1957.

Lumango (*Lagoa*), lake near Rio Bengo. 2 specimens. 14th November, 1957.

Panguila (*Lagoa*), large lake near mouth of Rio Bengo. 4 specimens. 8th and 9th November, 1957.

Bom Jesus, small lake on the banks of the Rio Cuanza. 10 specimens. 13th November, 1957.

Cabungabunga (*Lagoa*), large lake on the flood plain of the Rio Cuanza. 8 specimens. 13th November, 1957.

Dalagosa (*Lagoa*), lake on flood plain of Rio Cuanza. 189 specimens. 13th November, 1957.

Guimbe (*Lagoa*), large lake near Rio Cuanza. 4 specimens. 13th November, 1957.

Quequesse (*Lagoa*), grass-choked swamp on flood plain of Rio Cuanza. 5 specimens. 13th November, 1957.

Moembege (2) (*Rio*), two localities : (1) backwater about one kilometre upstream from Salazar, 4 specimens ; (2) Washing point in river in Salazar, 5 specimens. 30th November, 1957.

Quionqua (1), marshy roadside pool about two kilometres north of village on road to Duque de Braganza falls. 31 specimens. 25th October, 1957.

Quissol (2) (*Fazenda*), dammed pool in Quastimbala stream. 8 specimens. 24th October, 1957.

HABITAT. This species is extremely common throughout the coastal plain and was also found in the escarpment region at Salazar and on the plateau in the Malange district. In these areas *B. globosus* was found in a wide variety of habitats, large lakes, small pools (some possibly temporary) and in gently moving water in irrigation ditches and small rivers. The species is normally found on aquatic vegetation, particularly water lilies, but is also often found on muddy bottoms in shallow water and the specimens from Lagoa Quilunda were mostly collected from wet flotsam along the water's edge on a beach of limestone shingle. *B. globosus* was found associated with all of the other species which occur in the same area except *Burnupia* sp. but it was most often found together with *Bulinus forskali* and for this reason its absence from Lagoa Cabemba is interesting.

SHELL (Pl. 9, figs. 1–5). Medium to large, globose, spire not pronounced but in older specimens the body whorl descends considerably relative to the penultimate whorl, aperture roughly oval, outer lip meeting the body whorl usually nearly at a right angle, columella truncate but the truncation sometimes poorly defined, callosity a little lighter in colour than the shell, columellar margin reflexed either completely to the body whorl or leaving a narrow umbilical slit. The colour is usually pale yellowish-brown but sometimes darker ; clean shells are shiny and the sculpture consists of fine growth lines, occasionally with a more marked pattern of fine wavy lines.

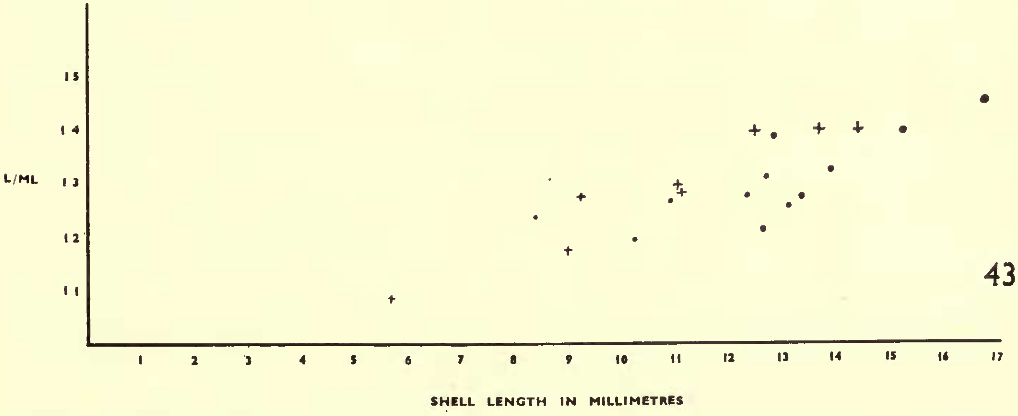


FIG. 43. Mean value of the ratio shell length/aperture length plotted against mean shell length for population samples of *Bulinus globosus* (*) and *B. africanus* (†).

The following table gives some of the dimensions in millimetres of a number of samples and Text-fig. 43 shows the mean value of the ratio shell length/aperture length plotted against mean shell length for populations of this species and of *B. africanus*.

Locality	Mean Length (Range in Brackets)	Mean Width	Mean Value l/ml (Range in Brackets)
Tentativa 1	13·1 (6·9–15·5)	10·1	1·25 (1·13–1·37)
Tentativa 2	10·9 (8·8–12·3)	8·4	1·26 (1·12–1·37)
Matoz	12·7 (4·3–16·6)	9·8	1·30 (1·17–1·44)
Libongo	16·8 (15·2–19·4)	10·6	1·45 (1·37–1·55)
Dalagosa	12·3 (6·0–18·0)	8·9	1·27 (1·06–1·46)
Bom Jesus	8·3 (4·0–16·2)	6·5	1·23 (1·13–1·41)
Quequesse	15·2 (12·8–18·4)	10·6	1·39 (1·35–1·45)
Cabungabunga	10·2 (7·1–15·5)	7·3	1·19 (1·10–1·37)
Quilunda	12·3 (5·75–15·7)	9·1	1·27 (1·06–1·42)
Lalama	13·9 (10·1–16·0)	10·7	1·32 (1·21–1·41)
Moembege	13·3 (11·7–14·4)	9·5	1·27 (1·20–1·34)
Quissol	12·6 (9·7–14·4)	9·1	1·21 (1·07–1·33)
Quionqua	12·8 (10·4–13·9)	8·9	1·38 (1·18–1·49)

ANATOMY. The mantle in fully grown specimens is usually uniformly black with a grey edge but in younger individuals it is pale grey with large black blotches. These pigmented patches increase in size until they coalesce and cover the whole mantle surface. The renal ridge on the underside of the mantle is almost always present in some form ; it may appear as a distinct crest running the length of the kidney or it may extend for only a short distance as no more than a slightly thickened median ridge. The intermediate ridge is well developed and roughly as long as the kidney.

The male copulatory organ is large, its length increases with shell length and the ratio of the length of penis sheath to that of preputium remains roughly constant at all growth stages. The mean value of this ratio in 147 specimens dissected from Lagoa Dalagosa is 0·83 and the range is from 0·56–1·50. The maximum width of the sheath is always less than that of the preputium and occurs as a regular dilatation near to the proximal end (Text-figs. 45–48, 50, 51). The preputium is darkly pigmented distally but the dark colour does not usually extend up to the junction with the sheath. The prostate grows steadily with increase in shell size up to a shell length of about 13 mm. and then the rate decreases but the accessory female glands appear to develop rapidly at a shell length of about 12 or 13 mm. The vagina is of medium length and the receptaculum seminis is globose in recently matured forms and about equal in diameter to the length of its duct (Text-figs. 44, 49). In older specimens the receptaculum becomes very distorted by the pressure of the accessory female glands.

Of the 147 specimens dissected from the Dalagosa population 36 per cent. were found to be infected by larval trematodes. The infection rate was highest in the larger size groups but this is probably due to immature infections in younger individuals being overlooked. The state of preservation of the material did not permit a detailed study of the larvae.

RADULA. There are six to eight tricuspid laterals in each half row, three or four transitional teeth and about twenty marginals. The cusps on the laterals are roughly triangular, broad-based and of medium length (Text-fig. 52). The endo- and mesocones are of approximately equal length and the ectocone is normally about two-thirds the length of the mesocone. Aberrations are particularly common amongst the coastal plain populations, interstitial cusps in the centrals and on either side of the mesocone in the laterals are frequently found (Text-fig. 53), also sub-division of the endocone in all of the laterals. Another common aberration is a corrugation of the inner margin of the endocone on the inner laterals. Very small accessory cusps above either the endo- or ectocones are seen but are not as common as they are in *B. forskali*.

The type-locality for *B. globosus* is lakes on the banks of the Rio Dande, Angola. In Welwitsch's day the flood plain of the Dande must have been rather similar to that of the Cuanza at the present time with large, shallow lakes covering considerable areas during the dry season and joining to make an almost continuous stretch of water during the rains. Now however, the Mabubas dam which supplies Luanda with hydro-electric power has been thrown across the river above Caxito and the former flood plain below the dam is largely occupied by the sugar plantations of the Fazenda Tentativa. The " type habitat " of *B. globosus* therefore no longer exists but the species is common in the irrigation system of the plantation and in the stream which flows past the sugar refinery. Specimens from these places compare well with those in the type series (Pl. 5, figs. 6, 7) but none of the partially umbilicate forms (of which there are some specimens in the original series (Wright 1957)) was found. Morelet mentions that the species was also obtained by Welwitsch from the area of Moembege in the Cazengo district and it is possible that the aberrant specimens may have come from there and been mixed with the material from the Dande.

Both Connolly (1928) and Wright (1957) remarked on the poor development of the characteristic microsculpture of this species-group in Angolan specimens and this observation is confirmed by examination of further material. It is only well marked in a few young individuals and does not seem to persist on the later whorls as in material from Sierra Leone and other West African territories.

Carvalho and Janz (1960) record *B. globosus* from the drainage systems of the Zaire (Congo), Cuanza, Zambesie, Catumbela and Cunene (at Nova Lisboa). The samples on which their description is based are not large but they remark on (and figure) a considerable range of variation in the radula teeth and the constancy of the penis-sheath being shorter and narrower than the preputium. They remark on the absence of the species in many places in the east where the soil is sandy and the waters clean and note that it prefers stagnant water with decomposing organic material.

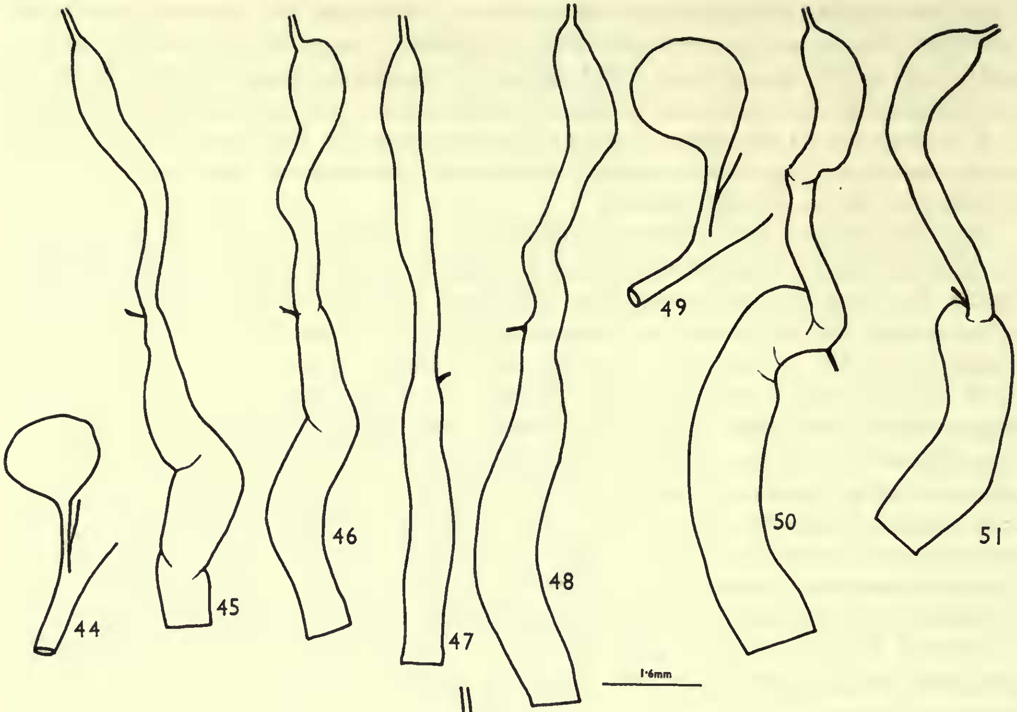
Bulinus africanus (Krauss)

Physopsis africana Krauss, 1848: p. 85, pl. 5, fig. 14.

MATERIAL

Cangombe, Huila Province, pools in stream bed. 15 specimens. 21st November, 1957.

Capembe and San Jose, Huila Province, seepage ditch. 9 specimens. 21st November, 1957.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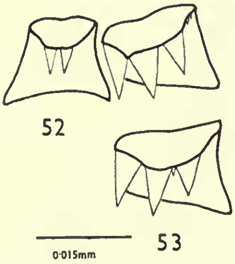
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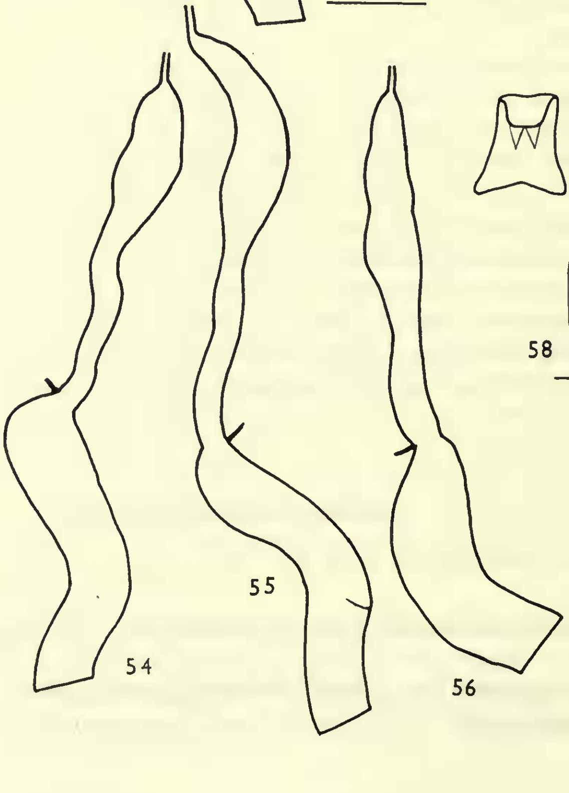

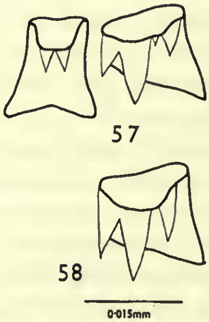
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Cassinde Pequeno, Huila Province, small pools formed by surplus water from an open well. 34 specimens. 21st November, 1957.

Cassinga, Huila Province, backwater in Rio Cului. 3 specimens. 22nd November, 1957.

Cativa, Huila Province, washing place in Rio Cuando. 10 specimens. 23rd November, 1957.

Cului (Rio), Huila Province, bridge on Vila Artur de Paiva-Dongo road. 2 specimens. 23rd November, 1957.

Dongo, Huila Province, pools on margin of Rio Cubangue. 9 specimens. 23rd November, 1957.

Gunda Vunjanga, Huila Province, deep pool in stream bed. 7 specimens. 22nd November, 1957.

Quesso, Huila Province, two localities. (1) Irrigation system of Granja Administrativa. 7 specimens ; (2) Marshy ground behind raised bank of Rio Cubango near washing place. 18 specimens. 21st November, 1957.

Senga, Huila Province, washing place in stream. 2 specimens. 22nd November, 1957.

Vila Artur de Paiva, Huila Province, ditch carrying surplus water from spring at main water point in town. 22 specimens. 21st November, 1957.

HABITAT. *Bulinus africanus* was found in nearly all of the localities visited in the neighbourhood of Vila Artur de Paiva in Huila Province. At the time when collections were made the rains were just beginning and water levels were low but all of the habitats were either in flowing water or pools in stream beds or ditches which would flow when the rains are at their height. In some places such as the seepage ditch at Capemba and San Jose and at Cassinde Pequeno the snails were collected in trickles of water so shallow that the shells were not fully covered but in most places they were found on aquatic vegetation.

SHELL (Pl. 4, figs. 6–8). The general appearance of the shell is similar to that of *B. globosus* but the outline is more ovoid, the spire is usually exserted and pointed, the aperture is more pronounced and the callosity is often whiter. The reflection of the columellar margin is similar to that in *B. globosus* in that there may be a narrow umbilical slit or it may be totally occluded.

The table gives some of the mean dimensions of the larger samples from populations studied.

FIGS. 44–53. *Bulinus globosus.* Figs. 44 & 49 receptacula and Figs. 45–48 male copulatory organs of specimens from Lagoa Dalagosa. Fig. 50. Male copulatory organ of specimen from Fazenda Libongo. Fig. 51. Male copulatory organ of specimen from Fazenda Tentativa. Figs. 52 & 53. Radula teeth.

FIGS. 54–58. *Bulinus africanus.* Figs. 54–56. Male copulatory organs of specimens from Cassinde Pequeno. Figs. 57 & 58. Radula teeth.

Locality	Mean Length	Mean Width	Mean Ratio Shell Length/ Aperture Length
Casinde Pequeno	13 (11·3–16·8)	8·7	1·39 (1·23–1·51)
Cangombe	14·4 (8·8–18·0)	9·2	1·39 (1·13–1·72)
Quesso 2	12·5 (10·2–14·8)	7·95	1·39 (1·15–1·53)
Cativa	9·1 (3·2–20·0)	6·3	1·22 (1·05–1·45)
Vila Artur de Paiva	11·0 (6·5–16·8)	7·8	1·28 (1·11–1·48)
Dongo	5·7 (3·5–8·0)	4·5	1·08 (1·05–1·11)

The mean values of shell length/aperture length are plotted against mean shell length together with those for *B. globosus* in Fig. 43 and it can be seen that the values of this ratio in *B. africanus* from Huila tend to be rather higher at any given shell length than those for *B. globosus*, an expression of the greater exsertion of the spire in the present species.

On young, clean shells of *africanus* the micro-sculpture of fine wavy lines is usually more clearly marked than in the lowland *globosus*.

ANATOMY. The only anatomical character in which Angolan *B. africanus* has been found to differ from *B. globosus* is the male copulatory organ. The mean ratio of penis-sheath/preputium in 32 specimens from three of the populations examined is 1·04 with a range from 0·8–1·4. The maximum diameter of the sheath in *africanus* is about $\frac{1}{3}$–$\frac{1}{2}$ of its length from the proximal end and it does not occur as a smoothly regular dilatation as in *globosus* but as a rather irregular widening (Text-figs. 54–56). The preputium is usually marked with alternating bands of light and dark pigment.

RADULA. There are six to seven tricuspid laterals, three or four transitional teeth and about twenty marginals in each half row. The centrals tend to be narrower and slightly longer-cusped than those in *globosus* and the mesocones of the laterals are usually distinctly longer and more dagger-like. The endocones of the laterals are about two-thirds as long as the mesocones while the ectocones are only about one-third as long (Text-figs. 57, 58). There is often a slightly greater degree of fusion of the bases of the endo- and mesocones in *africanus* than there is in *globosus*. Aberrations similar to those in *globosus* have been seen in this species but are by no means so common.

Bulinus africanus was described by Krauss from material collected near Durban. According to Mandahl-Barth (1957b) its distribution is confined to Natal, Transvaal, Northern and Southern Rhodesia and probably also Mozambique and Southern Tanganyika. The present material does not agree in detail with Mandahl-Barth's description of *africanus*, particularly with respect to the proportions of the male copulatory organ. Mandahl-Barth illustrates the penis-sheath as being almost twice as long as the preputium and slightly wider but the material from Huila has the two parts of the organ more nearly equal to one another both in length and diameter. The cusps of the lateral radula teeth are certainly larger than those of *globosus* from the type-locality but there is no great difference in the size of the teeth themselves.

The shell characters are closer to *africanus* than *globosus*. The smaller angle at the upper end of the aperture was a character used by Pilsbry and Bequaert (1927) to distinguish *B. africanus* from the form which they considered to be its sub-species *B. a. globosus*. Mandahl-Barth (1957b) emphasizes the distinctness of the columellar truncation and its frequent accentuation by a strong white callosity in *africanus* but Connolly's (1939) criterion of the complete absence of an umbilical slit in *africanus* does not appear to be valid.

The occurrence of *B. africanus* in the southern upland region of Angola not associated with the very closely related *B. globosus* from the northern plateau and coastal plain is extremely interesting. The different distributions of the two species may be due to different ecological requirements but in view of their apparent sympatric distribution in south-east Africa this seems unlikely. It is more probable that the two species are derived from different geographical origins. In a discussion of taxonomic problems in *Bulinus* Wright (1961) mentioned the possibility that the *africanus* species-group had its origin somewhere in the Tanganyika region and that the species within the complex are no more than the terminal parts of clines radiating from this centre. It is significant that *B. africanus* is most clearly distinct in the eastern part of the Union of South Africa and that the drainage from the southern part of the Angolan plateau is connected with this region through the Okavango swamp in Bechuanaland. This suggests that *B. africanus* may have reached Angola by this route while *B. globosus* has spread by the more direct line from Tanganyika through Northern Rhodesia and Katanga to the northern part of the plateau and the coastal plain. According to Carvalho and Janz (1960) there are large areas in the extreme eastern part of Angola where no snails of the *africanus* group are found, due to unfavourable ecological conditions. This area may have served as a barrier to direct westward movement and forced a separation into the northern and southern routes suggested above.

Bulinus angolensis (Morelet)*

Physa welwitschi Morelet, 1866: p. 162. Morelet, 1868: p. 88, pl. 9, fig. 9.
Physa angolensis Morelet, 1866: p. 162. Morelet, 1868: p. 88, pl. 9, fig. 8.
Physa parietalis Mousson, 1887: p. 298, pl. 8, figs. 8 and 8a.
Bulinus tropicus angolensis; Carvalho & Janz, 1960.

MATERIAL

Catoco, Huila Province. Pools in stream bed. 78 specimens. 21st November, 1957.

Cangombe, Huila Province. Pools in stream bed. 3 specimens. 21st November, 1957.

Cului (Rio), Huila Province. 9 specimens. 23rd November, 1957.

Dongo, Huila Province. Pools on margin of Rio Cubangue. 28 specimens. 23rd November, 1957.

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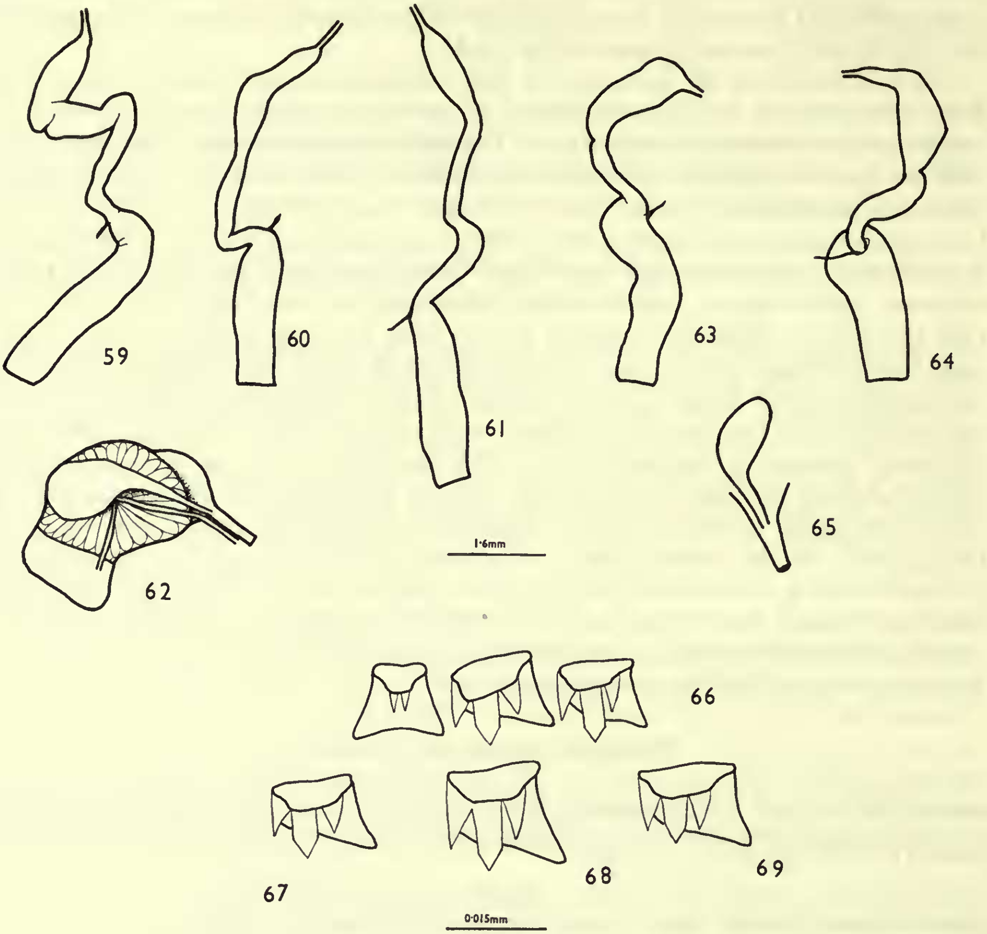
* On line-priority the name used for this species should be *B. welwitschi* but the name *angolensis* is better known and, since it is inevitable that further work on this complex in other parts of Africa will reveal facts necessitating further nomenclatorial changes, the more commonly used name has been retained to avoid unnecessary confusion.

Senga, Huila Province. Washing place in stream. 4 specimens. 22nd November, 1957.

Quissol (2) (*Fazenda*). Pool in Quastimbala stream, near Malange. 14 specimens. 23rd October, 1957.



Figs. 59–69. *Bulinus angolensis.* Figs. 59–61. Male copulatory organs of specimens from Dongo. Fig. 62. Receptaculum and prostate of specimen from Dongo. Figs. 63 & 64. Male copulatory organs of specimen from Quissol. Fig. 65. Receptaculum of young specimen from Quissol. Fig. 66. Radula teeth of specimen from Quissol. Fig. 67. First lateral radula tooth of specimen from Catoco. Fig. 68. First lateral radula tooth of syntype of *Bulinus welwitschi*. Fig. 69. First lateral radula tooth of syntype of *Bulinus angolensis*.

Habitat. All of the localities from which this species was collected were either gently flowing streams or pools in stream beds. The snails were always found on aquatic vegetation and never on the mud.

SHELL (Pl. 5, figs. 1–5). The shell in this species is very variable. It ranges from globose with a depressed spire to ovoid or almost oblong with a well developed spire. In large specimens the upper whorls are regularly ribbed while the later ones have only irregular growth lines but in small individuals the whole shell is regularly ribbed. The colour varies from light reddish-brown to almost colourless. The aperture is ovate in globose specimens with the outer margin regularly curved but in higher spired forms the outer lip is often flattened and almost straight. The columella is sometimes slightly twisted and the reflection of the columellar margin varies but all of the specimens examined were narrowly umbilicate. The following are the mean lengths together with the ratio shell length/aperture length of several of the populations examined :—

Locality	Length	Shell Length Aperture length
Catoco	9·15 (3·7–11·2)	1·27 (1·09–1·58)
Dongo	5·4 (2·72–7·8)	1·15 (1·04–1·26)
Cangombe	11·7 (11·2–12·8)	1·37 (1·32–1·45)
Quissol	5·5 (4·0–9·6)	1·17 (1·08–1·33)

ANATOMY. The mantle varies from almost white to light grey with regular, large black spots, often roughly circular. The intermediate mantle ridge varies in length between half and one-third that of the kidney. The male copulatory organ is variable in size and in the proportions of the penis-sheath and preputium. In the sample from Quissol five of the ten specimens dissected were aphallic and the sheath was longer than the preputium in those individuals with a copulatory organ (Text-figs. 63, 64), the maximum diameters of the two parts were approximately equal. The receptaculum seminis is clavate, its long axis is about equal in length to its duct which is in turn equal to the length of the vagina (Text-fig. 65). The samples from the southern part of the plateau show considerable variation in both the occurrence and proportions of the male copulatory organ. From Catoco two out of the seven dissected were aphallic and the sheath/preputium ratios in the others varied between about 2 : 1 and 3 : 2 (Text-figs. 59, 60). From Dongo two out of ten were aphallic and the proportions of the parts in the euphallic individuals ranged between about 3 : 1 and 2 : 1 (Text-fig. 61) while from the Rio Cului the five largest specimens (ranging in shell length from 4·0–4·8 mm.) were dissected and all were found to be aphallic. No aphallic individuals occurred in the two small samples from Senga and Cangombe and the proportions of the parts of the male organ varied between 3 : 2 and 5 : 3. Two of the three specimens from Cangombe were grossly infected with larval trematodes but no cercariae were found in a sufficiently good state of preservation to enable an identification to be made. One of the snails from Dongo was heavily infected with larval amphistome flukes.

RADULA. There are five to seven tricuspid laterals in each half-row and up to twenty marginals. The teeth are smaller than those in *B. globosus* and larger than those in *B. truncatus rohlfsi* but they are similar to those in *rohlfsi* in that the mesocone of at least the first lateral and often all of the laterals has the arrow-head shaped tip characteristic of the *truncatus* species group (Text-figs. 66, 67). Aberrations in the form of the teeth are fairly common, particularly an assymetrical development of the central and sub-division of the endocones of the laterals.

The material which has been available for this study is inadequate to assess properly the relationships of the species or even to make a proper description of its probable full range of variation. The most important fact which has emerged is the apparent relationship of *angolensis* to the *truncatus* group rather than to the *tropicus* complex to which it has so far been referred.

None of the specimens examined is conchologically close either to the type series of *angolensis* (Pl. 6, figs. 4, 5) or to that of *welwitschi* (Pl. 6, figs. 1–3) but many of the specimens from the southern plateau region resemble the illustration of Mousson's *parietalis*. Mandahl-Barth (1957b) tentatively refers *parietalis* to the synonymy of *angolensis* but he points out that it is not possible to be definite about this until material from the type locality of *parietalis* at Ondangua in Ovamboland (near the border between Angola and South-west Africa) is available. However, in a footnote on page 60 of his monograph (1958) he refers to material of *Bulinus truncatus* from Ondangua and the photograph of one of these specimens in a later paper by the same author (1960) shows it to be very like the types of *angolensis*. In the same paper Mandahl-Barth also illustrates a specimen of *B. truncatus* from Kalambo in the Congo and this shell, although larger, is similar to the largest specimen in my sample from Quissol. Bequaert and Clench (1933) recorded two dead specimens of *B. angolensis* from the Inkisi river near Kisantu, also in the lower Congo area. The type locality for *angolensis* is said to be in the district of Duque de Braganza towards the northern end of the plateau but Welwitsch himself was unable to reach this area and his manuscript notes on the specimens sent to Morelet contain a supplement mentioning several samples from this region which were collected by a friend in 1862-3 after Welwitsch had left Angola and in no case is the origin of the samples more clearly defined than by reference to the district. During the present expedition a number of localities in the Duque de Braganza area were searched but the only specimens found were those from Quissol, just south of Malange. The type locality for *welwitschi* is near the Bumbo river in the south of Angola in the Mossamedes area.

One of the syntype specimens of *angolensis* and two of the type series of *welwitschi* were found to contain dried remains of the original animals. By incubation for an hour at 28° C. in a 2 per cent. solution of tri-basic sodium phosphate (after the method of Van Cleave and Ross, 1947) the bodies were sufficiently soft to be removed from the shells. They were left for three days in 0·5 per cent. tri-basic sodium phosphate at room temperature and then dissected. The tissues were very brittle and accurate measurements of the male copulatory organs were not possible but that of *angolensis* had an approximate sheath/preputium ratio of 2 : 1 and one of the *welwitschi* was aphallic while the other had a penis complex similar to that of *angolensis*. The euphallic specimen of *welwitschi* was infected with amphistome cercariae apparently similar to those found in one of my specimens from Dongo. Preparations of the radulae from these three paratype specimens (Text-figs. 86, 69) showed them to be similar to those described from the recent material and all of them have the arrow-head shaped mesocone of the first lateral.

Carvalho and Janz (1960) have followed the usage of Mandahl-Barth and refer to *angolensis* as a sub-species of *B. tropicus.* They have studied specimens from a number of localities and have found them to be widely variable. A large sample from Tchivinguiro near Sa da Bandeira was unlike any of the others in that the shells were high spired with acute apices and for this sample of 165 specimens the authors worked out the ratio of aperture length/shell length for all of the specimens. The ratio plotted as a frequency distribution gives a normal Gaussian curve with its lowest value at 0·3 and its highest at 0·7 with the median at 0·483. This emphasizes very strongly the enormous variation in shell shape within a population of this species. In the general anatomical description Carvalho and Janz make no mention of finding aphallic specimens and they illustrate an aberrant individual with two penis sheaths and only a single preputium. The radula is not mentioned in the text but a figure of the central and first lateral of a specimen from the Tchivinguiro sample shows the mesocone of the lateral to be a simple conical cusp.

The distinctions between the *truncatus* and *tropicus* groups are not as clear-cut as has been suggested in the past and study of this Angolan material has led to an investigation of the two main distinguishing characters in some other material. Mandahl-Barth (1957b) records aphallic specimens of *tropicus* in Northern Rhodesia but these may be an extension of the range of *angolensis.* The form of the mesocone of the lateral radula teeth cannot be regarded as diagnostic for the radulae of the paratypes of *B. tropicus* and *B. diaphana* in the Piele collection both have the mesocone cusp as arrow-head shaped as it is in such species as *B. truncatus rohlfsi* and *B. sericinus.* Only examination of a great deal more material will indicate whether *B. angolensis* is truly a member of the *truncatus* group or an aberrant *tropicus* or if it is genuinely a connecting link between the two groups.

Bulinus truncatus rohlfsi (Clessin)

Physa rohlfsi Clessin, 1886: p. 349, pl. 49, fig. 7.
Bulinus truncatus rohlfsi; Mandahl-Barth, 1957(b).

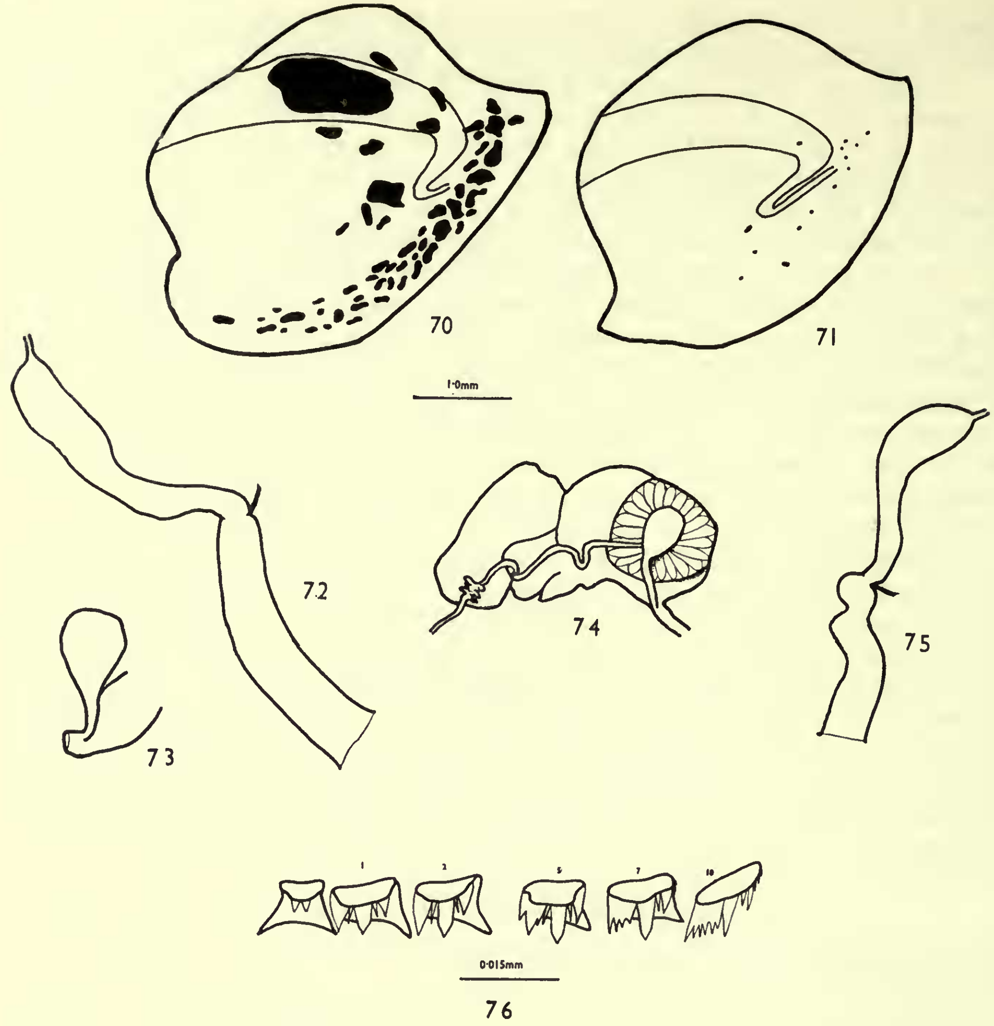
MATERIAL

Panguila (*Lagoa*), north-west corner of lake near the mouth of the Rio Bengo. 8 specimens. 9th November, 1957.

Cabemba (*Lagoa*), large lake on flood plain of Rio Cuanza. About 150 specimens. 14th November, 1957.

HABITAT. In both localities this species was found associated with *B. forskali* on *Ceratophyllum* at all levels in water to a depth of about three feet near the lake shore and in Lagoa Cabemba on an open shore exposed to gentle wave action.

SHELL (Pl. 11, figs. 8–19). Almost rectangular in outline with a low spire and smoothly rounded whorls. The outer lip of the aperture is nearly straight and only slightly curved, it meets the body whorl almost at right angles. The columella is more or less straight and the columellar margin is reflexed so that the umbilicus



Figs. 70–76. *Bulinus truncatus rohlfsi*. Figs. 70 & 71. Heavily marked and lightly marked mantles. Figs. 72 & 73. Male copulatory organ and receptaculum of laboratory-bred specimen from Lagoa Cabemba stock (7·3 mm. shell-length). Figs. 74 & 75. Accessory genital glands and male copulatory organ of wild specimen from Lagoa Cabemba (5·1 mm. shell-length). Fig. 76. Radula teeth.

is closed. The specimens from Panguila are white and shiny while those from Cabemba are shiny, translucent and almost colourless. The sculpture consists of regular poorly developed ribs mostly on the upper whorls while on the body whorl there are usually only fine growth lines. The longest specimens in both samples were 6·4 mm. long, 5 mm. wide, 5·2 mm. aperture length and 3·2 mm. aperture width and the majority fell within the 4–5 mm. shell length range.

ANATOMY. The mantle pigmentation varies from a number of dark grey or black blotches, particularly in the area overlying the kidney, with a series of smaller black markings inside the mantle border, to completely white and all intermediate forms occur (Text-figs. 70, 71). The intermediate ridge between the kidney and rectum is short, not more than half the length of the kidney and seldom more than a third as long.

All of the specimens from Panguila were dissected and found to be aphallic and only eight out of forty of those examined from Cabemba had a fully developed male genital system. The copulatory organ, when present, is large, roughly 5 mm. long in a specimen of 6 mm. shell-length. The penis sheath and preputium are roughly equal in length but the sheath is sometimes a little longer (Text-figs. 72, 75). The proximal dilatation of the sheath is about equal in diameter to the preputium and it occupies about a third of the length of the sheath. The penis is large and folded within the dilated part of the sheath which is often transparent and the epiphallus is about half to two-thirds the length of the sheath. The development of the rest of the male genital system is variable, in aphallic specimens there may be no trace of sperm duct, prostate or vas deferens while in others there may be a relatively well developed sperm duct and a rudimentary prostate. Even in euphallic individuals the prostate never attains the relatively large size that it reaches in members of the *forskali* and *africanus* species complexes. The sperm duct in normal specimens is about twice the diameter of the vas deferens and is moderately convoluted ; in aphallic individuals the sperm duct, if present, is narrower and almost straight. The seminal vesicle has small tuberculate projections and is situated near the distal end of the hermaphrodite duct, about one third of the duct length from the carrefour. The translucent funnel beneath the ovotestis at the proximal end of the hermaphrodite duct is rather longer than in most bulinids, approximately equal in length to one third of the duct.

The vagina is short and slightly bulbous, the receptaculum seminis duct opens into it near its junction with the uterus. The receptaculum is almost globular and its diameter is roughly equal to the length of its duct (Text-figs. 73, 74). The uterus and its associated glands are relatively large and the oviduct is wide and scarcely convoluted. The accessory female glands in aphallic individuals appear to be fully developed and functional at a shell-length between 4·5 and 5·0 mm.

RADULA. There are 20–25 teeth in each half-row of the radula, five or six of which are tricuspid laterals. In a number of radulae from both Panguila and Cabemba small interstitial cusps were found to be present on either side of the mesocone in all of the laterals and sub-division of the endocone of even the first lateral was observed in several specimens. The mesocones of the laterals are relatively long and broad and arrow-head shaped at the tip (Text-fig. 76).

The status of the sub-species *B. truncatus rohlfsi* is still dubious and a great deal of work is needed to elucidate its relationships. The present material is referred to this sub-species with some reservations, particularly in the light of the finding that *B. angolensis* is also a member of the *truncatus* group. Comparison with specimens from Lake Barombe Mbo in the Cameroons shows no significant differences.

Material of *rohlfsi* from the neighbourhood of Ibadan in Nigeria has a higher spire and darker coloured shell. Both the Nigerian form and that from Lagoa Cabemba have been bred in the laboratory for over three years and the two cultures retain some of the distinctions that were apparent in the original stocks although the appearance of both forms has been modified by laboratory breeding conditions. The changes which have occurred in the Angolan form are similar to those observed by Schwetz (1954) in a laboratory bred population of *Bulinus coulboisi* originating from Lake Tanganyika and the resemblance in shell-form between the wild stocks of both Schwetz's material and that from Cabemba is very marked. Mandahl-Barth (1957b) comments on the extremely close similarity between *B. coulboisi* and *B. trigonus* apart from the characters of the radula teeth which have simple triangular mesocones on the laterals in *coulboisi* but arrow-head shaped cusps in *trigonus*. On these grounds the present material is in many respects similar to *trigonus* and the question of the relationships between the lake forms of the *truncatus* group and the more widely distributed *rohlfsi*-like forms merits investigation. This point is further emphasized by Mandahl-Barth's (1960) remarks on the conchological similarity between specimens of *B. truncatus* (now referred to *B. angolensis*) from Ovamboland and *B. transversalis* from Lake Victoria.

Larambergue (1939) showed that the aphallic condition in *Bulinus truncatus* is a genetically controlled character and that the proportion of aphallic to euphallic individuals in a population is a more or less constant character. He also demonstrated that the degree of pigmentation of the mantle is genetically controlled and that the blotched form is dominant to the unmarked. Although no controlled experimental work has been carried out on the Angolan material the question of the simple dominance of the blotched mantle is questionable since by far the greater proportion of individuals examined have intermediate degrees of pigmentation and the number of heavily marked specimens only slightly exceeds the number of unmarked. One thing is certainly clear and that is the absence of linkage between mantle pigmentation and the condition of the male copulatory organ for both blotched and unmarked individuals have been found to be euphallic.

Laboratory bred specimens of the material from Lake Cabemba have been successfully infected with *Schistosoma haematobium* from both Cairo and Khartoum. The Angolan snails appear to be as susceptible to infection as the " normal " hosts for each strain from the point of view of the proportion of exposed individuals which shed cercariae but they produced less cercariae and appeared to lose the infection after shedding more easily than the normal hosts. The cercariae from the Cabemba snails were infective to hamsters which subsequently passed viable eggs.

Bulinus forskali (Ehrenberg)

Isidora forskalii Ehrenberg, 1831: p. 20.
Bulinus schmidtii Dunker, 1853: p. 9, pl. 2, figs. 7, 8.
Physa capillacea Morelet, 1868: p. 89, pl. 8, fig.1.
Physa apiculata Morelet, 1868: p. 90, pl. 8, fig. 3.
Physa semiplicata Morelet, 1868: p. 91.
Physa turriculata Morelet, 1868: p. 92, pl. 9, fig. 7.

Physa clavulata Morelet, 1868: p. 93, pl. 9, fig. 6.
Physa moreleti Nobre, 1905: p. 15, pl. 1, figs. 29, 30.
Physa osorioi Nobre, 1905: p. 15, pl. 1, figs. 31, 32.

MATERIAL

Bom Jesus, small lake on banks of Rio Cuanza. 17 specimens. 13th November, 1957.

Cabemba (*Lagoa*), large lake on flood plain of Rio Cuanza. 8 specimens. 14th November, 1957.

Cabungabunga (*Lagoa*), large lake on flood plain of Rio Cuanza. 17 specimens. 13th November, 1957.

Dalagosa (*Lagoa*), lake on flood plain of Rio Cuanza. 66 specimens. 13th November, 1957.

Dondo, Rio Mucoso. 38 specimens. (Sample received from Dr. Morais de Carvalho). 3rd July, 1957.

Guimbe (*Lagoa*), large lake on flood plain of Rio Cuanza. 26 specimens. 13th November, 1957.

Lalama (*Lagoa*), lake near junction of Rio Calucala and Rio Bengo. 12 specimens. 14th November, 1957.

Lumango (*Lagoa*), lake near Rio Bengo. 1 specimen. 14th November, 1957.

Panguila (*Lagoa*), lake near the mouth of the Rio Bengo. 2 samples :—(a) pool on the bank near the south-west corner of the lake. 26 specimens. 8th November, 1957 ; (b) North-west corner of the lake itself. 100 + specimens. 9th November, 1957. Also laboratory-bred material from the same stock.

Quilunda (*Lagoa*), large lake on the banks of the Rio Bengo. 40 specimens. 14th November, 1957.

Fazenda Tentativa, irrigation ditches on sugar plantation. Not many specimens collected but laboratory-reared material examined.

Matoz (*Lagoa*), small lake on the edge of the Fazenda Tentativa, on the Rio Dande drainage. Specimens collected from a small seepage ditch beside the lake. 10 specimens. 8th November, 1957.

Cuije (*Rio*), small pool on flood plain of the river. 5 specimens. 24th October, 1957.

Quionqua (2), small pool beside road. 4 specimens. 25th October, 1957.

HABITAT. The habitat of the material from Dondo is unknown. All of the other localities on the Cuanza flood plain are basically similar and the snails were either collected from the under side of waterlily leaves or from amongst *Ceratophyllum* which was present in most of the lakes. The habitat in Lagoa Panguila was similar and the specimens from the pool on the banks of the lake were collected from emergent grass. The material from Lagoas Lumango and Lalama was found in the wide surrounding reed bed which was present in both of these lakes. Lagoa Quilunda is unique amongst the lakes visited in that it apparently contains little aquatic plant life and has a stony bottom and beach with occasional tufts of emergent grasses. The snails were found on the grass or among debris washed-up along the water's edge. The material from Lagoa Matoz was found in a shallow (4–6″) seepage ditch beside the lake. The pool on the flood plain of the Rio Cuije was about four feet across and only 4–5″ deep with full sun exposure, almost certainly a temporary pool, and that near Quionqua was about three feet deep, slightly shaded, with a thick mud bottom and rotting vegetation ; the snails were found on emergent grasses in both places.

SHELL (Pl. 8, figs 1–16). There is a great range of variation in shell-form within this species but there are certain more or less constant characters. The upper whorls are nearly always ribbed and carinate, the carination forming a well-defined shoulder on the upper part of the whorl. The exsertion of the spire is a slightly variable character. The specimens from Dondo have strongly ribbed and shouldered upper whorls but the body whorl is often smoother and lacks the carination. The other samples from the Cuanza flood plain (Bom Jesus, Cabemba, Cabungabunga, Dalagosa and Guimbe) are very similar to one another. The shells are yellowish, thin, strongly ribbed and shouldered and, where the ribs join the shoulder the periostracum is produced into quite well-marked spines. The material from Panguila is similar but the shells are mostly colourless, the carination is not so well-marked and in many the spiral punctate pattern of the embryonic shell is continued on to the second and third whorls becoming modified into a faint spiral sculpture superimposed on the ribbing. In the sample from Quilunda the shells are thicker than any of the others, colourless and transparent and some are strongly ribbed and carinate while others are smoother and scarcely shouldered. The material from Lalama and Matoz is similar in the variability of the shouldering and that from Fazenda Tentativa (laboratory bred) shows few shouldered specimens although all are quite strongly ribbed. The few individuals from the pool near the Rio Cuije are well ribbed and shouldered on the upper whorls but all the specimens show a dark band (probably the remains of a peristome formed during aestivation) and below this band there is scarcely a trace of either ribbing or carination. The specimens from Quionqua are all ribbed and shouldered and two of them show small shoulder spines.

Variation in the degree of exsertion of the spire in different populations is well shown in Text-fig. 77 in which the mean values of the ratio shell length/aperture length are plotted against shell length. A number of interesting points are illustrated by this graph. First, the populations from the flood plain of the Rio Cuanza show a slightly lower ratio than those from around the Rio Bengo, indicating that they have a more squat appearance, second, there is an appreciable difference in the ratio between specimens from the pool on the banks of the Lagoa Panguila and those from the lake itself and lastly, the ratio is lower in specimens bred in the laboratory from the lake form than it is in the original wild sample. It can also be seen that the size range of the different samples varies considerably despite the fact that the collections (with the exception of the laboratory bred material from Panguila and the sample from Dondo) were all made within a period of a week. The following table gives the mean shell length and its range for some of the samples:

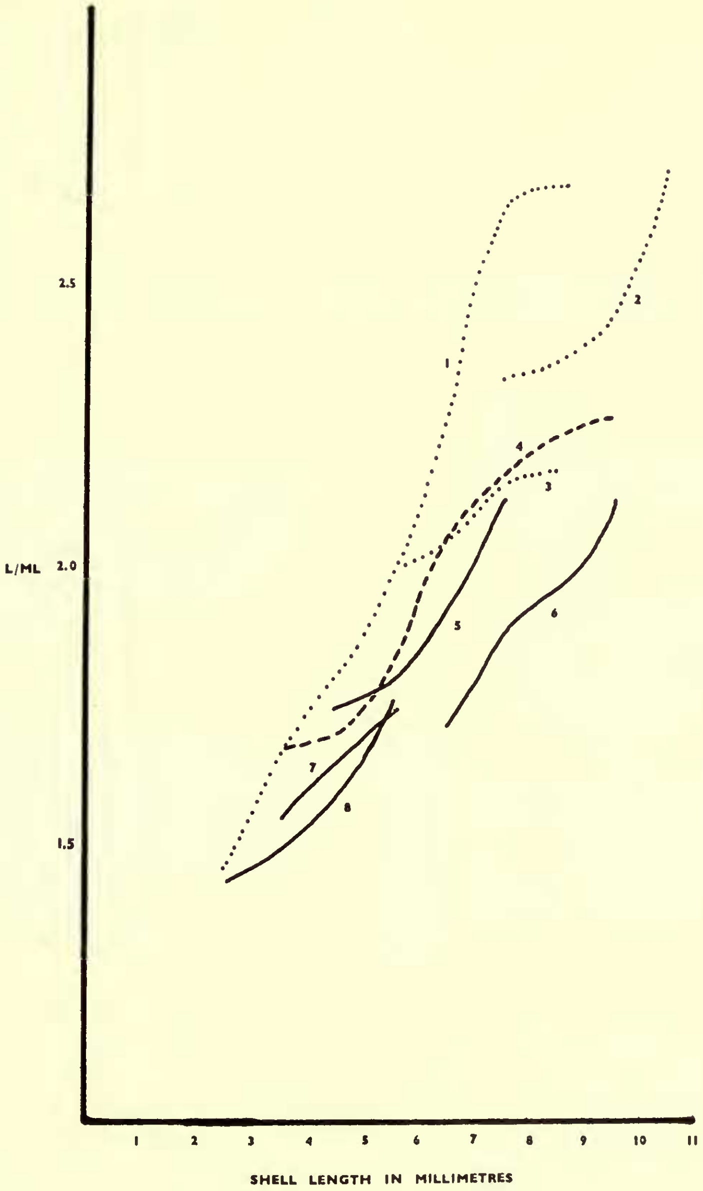


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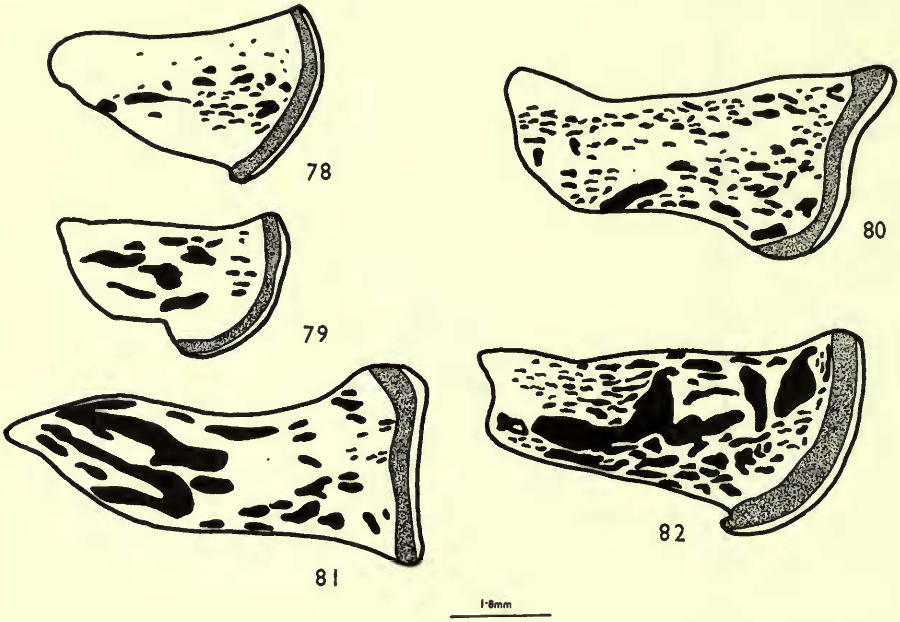
FIG. 77. The ratio shell length/aperture length plotted against shell length for population samples of *Bulinus forskali*. 1. Lagoa Panguila, north end of lake. 2. Lagoa Panguila, pool on edge of lake. 3. Lagoa Panguila, laboratory bred. 4. Lagoa Quilunda. 5. Lagoa Cabungabunga. 6. Dondo. 7. Lagoa Guimbe. 8. Lagoa Dalagosa.

Locality	Maximum Length	Minimum Length	Mean
Bom Jesus	9·5	3·0	5·7
Cabemba	5·1	2·7	4·1
Cabungabunga	7·4	4·0	5·9
Dalagosa	6·1	2·5	4·1
Guimbe	5·1	3·0	4·0
Quilunda	9·8	3·0	5·9
Panguila (pool)	11·5	7·0	8·8
Panguila (lake)	7·0	2·2	4·2

These figures are of little value without some indication of the maturity of the population and this will be discussed under the anatomical part of this description.



Figs. 78–82. *Bulinus forskali* mantles. Figs. 78 & 79. Lagoa Dalagosa. Figs. 80 & 81. Lagoa Quilunda. Fig. 82. Dondo.

Anatomy. The markings of the mantle vary considerably between individuals of the same population but there are definite trends in the distribution of the pigment which are associated with other differences between populations. The basic pattern consists of a light grey ground colour with a fairly wide darker grey band near the margin and a light grey or creamy edge. In those forms with strongly ribbed and carinate shells there are usually fewer dark markings than in the less shouldered populations but in these smoother forms there may be less actual pigment present although it is more widely distributed (Text-figs. 78–82). In the forms with a few dark markings the pigment is usually concentrated over the kidney.

The male copulatory organ is also variable. The penis sheath is a little longer than the preputium, in most populations the proportion is roughly 4 : 3 or 3 : 2 but in the sample from Dondo it approached 2 : 1. The maximum diameter of the dilatation of the sheath is about equal to the diameter of the preputium and lies about a quarter to one third of the sheath length from its proximal end (Text-figs. 83–90). The epiphallus is always short, about one third of the length of the sheath.

The female genital system shows no characters of sufficient constancy to merit consideration from a taxonomic point of view. The appearance of the receptaculum seminis varies greatly according to the age of the individual but in recently mature specimens it is ovate and the length of the dilated part is a little longer than the duct.

The main interest in the genital anatomy of these snails is in determining the state of maturity of the specimens and from this trying to obtain some idea of the reproductive activity of the populations. In *Bulinus jousseaumei* Wright (1957) has shown that there is a connection between the development of the accessory genital glands and the increase in the ratio shell length/aperture length. It has also been shown (Wright 1960) that there is an increase in shell length in *B. forskali* associated with the onset of maturity. In both cases these relatively sudden changes in growth rate are necessary to provide a greater shell volume to accommodate the accessory genital glands. The development of these glands is protandrous, the prostate becomes clearly defined and apparently functional before the muciparous and oöthecal glands of the female system are properly differentiated. In the fully mature adult snail the total volume of the accessory female glands exceeds that of the prostate by about three times, but egg-laying may have started before this when the prostate is about half the size of the female glands. This is taken as a rough index of the attainment of reproductive maturity, and the observations reported here are based on this criterion. At shell length 3·0–3·5 mm. the snails from Dalagosa and Guimbe have fully developed prostates and are mature between 4·0 and 4·5 mm., while those from Cabungabunga and Bom Jesus do not reach maturity until they have attained a length of 7·0–8·0 mm. The largest specimen from Cabemba was 5·1 mm. long and showed no appreciable development of the female glands. These samples come from relatively close localities and were all collected in two days. The specimens from Dondo reach maturity at a length of 7·0–8·0 mm. as do those from Quilunda and Lalama. The sample from Panguila (lake) are mature at about 6·5–7·0 mm. The results fit well with those anticipated from the form of the curves in Text-fig. 77 and emphasize the dangers of using absolute shell length as a criterion of maturity in this species. Whether these effects are ecological or genetically controlled remains to be determined.

RADULA. Teeth from a typical radula are illustrated in Text-fig. 91. The majority of the specimens examined had six tricuspid laterals and about fifteen marginals but there is a good deal of variation in these numbers which is not necessarily related to the size of the snail (small individuals may have as many as nineteen marginals while larger specimens may have only twelve or thirteen). Nearly all of the radulae examined showed small interstitial cusps between the main cusps of the laterals and the majority also had small accessory cusps on the inner margin of the endocone or on the outside of the ectocone. A large proportion of radulae with regularly malformed teeth were observed and these were more common in some populations than in others, the proportion of aberrant specimens being particularly high in the sample from Bom Jesus and some of these are illustrated in Text-figs. 92–95.

Bulinus forskali is well known as one of the most variable species of freshwater snail in Africa and this accounts for the large number of named species which have subsequently been shown to be extreme forms of *forskali*. The relatively long list of synonyms at the beginning of this description shows that the species is particularly variable in Angola. The names given by Morelet are convenient terms for referring to forms of the species because each of Morelet's " species " is based on an extreme development of particular characters. It is useless to think in terms of *B. forskali* from the Nile delta (the type locality) as being typical of the species but it is helpful to consider the dominant form in any region as being the most characteristic for that area. From a study of material collected during this expedition it is apparent that Morelet's *capillacea* (Pl. 7, figs. 4, 5) is the most commonly occurring form in Angola. All of the specimens from the Cuanza flood plain are very close to this form in their smaller size ranges, and the samples from Bom Jesus and Dondo clearly establish that *clavulata* (Pl. 7, figs. 11–14), *turriculata* (Pl. 7, fig. 10) and *schmidti* (Pl. 7, figs. 1–3) are merely extreme developments of this basic form at larger sizes. The forms *apiculata* (Pl. 7, figs. 6–10) and *semiplicata* (Pl. 7, figs. 15–17) are simply growth stages of the poorly carinate variety, they occur in mixed populations with the *capillacea* type in Panguila, Quilunda, Lalama and Fazanda Tentativa where they show all stages of intergrading. An examination of the type localities recorded for Morelet's species shows that there is probably a frequent shift in the dominance of any one form in a particular place. For instance, the type locality of *capillacea* is Libongo on the Rio Lifune and it is also recorded from Lagoa Quifandongo near the Rio Bengo but not from the Cuanza area where it is now the dominant form. *B. apiculata* and *semiplicata* were both originally described from the Cuanza drainage where neither form was found during this investigation (Morelet's description of *semiplicata* gives the origin of the material as pools near Mopopo, Rio Caranxa, but Welwitsch's manuscript notes definitely say " Rio Cuanza "). Mandahl-Barth (1957b) refers to *schmidti* as the form of *forskali* characteristic of the Angolan and Lower Congo region but this is not strictly true as *schmidti* is more obese and less markedly carinate than the commonest form in the area (Pl. 7, figs. 1–3). It has not been possible to examine the original material of Nobre's species *moreleti* and *osorioi* and so no definite conclusions about the affinities of these forms can be reached. From the illustrations it appears that *moreleti* is one of the strongly ribbed and carinate forms while *osorioi* resembles *apiculata*.

Carvalho and Janz (1960) mention the wide distribution of *B. forskali* in Angola and state that it is normally found in the shallow water of lakes or small streams.

Bulinus scalaris (Dunker)

Physa scalaris Dunker, 1845: p. 164.
Bulinus scalaris Dunker, 1853: p. 8, pl. 2, figs. 5, 6.
Physa canescens Morelet, 1868: p. 90, pl. 9, fig. 3.
Physa benguelensis Sowerby, 1873: pl. 9, fig. 77.

MATERIAL. Three specimens only, collected in a pool, Quionqua (1), about fifty kilometres north-north west of Malange on the road to the Duque de Braganza falls. 25th October, 1957.

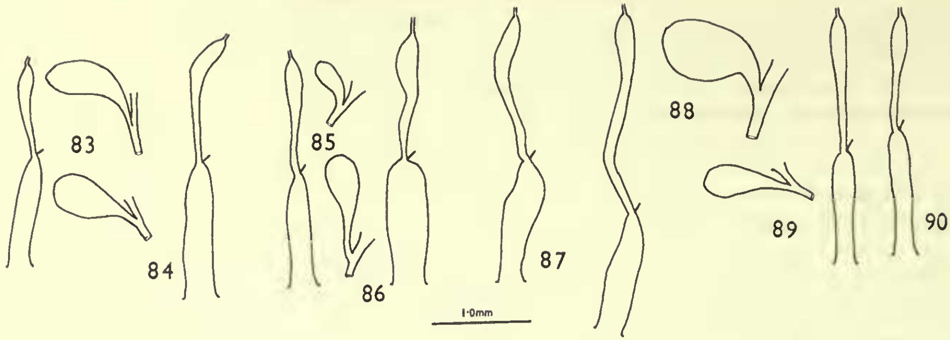
HABITAT. The pool was by the roadside, shallow and choked with grass, fully exposed to the sun and probably not permanent. At the time of the collection the rains had just begun and the pool appeared to have become only recently filled. *Bulinus globosus* was also found.

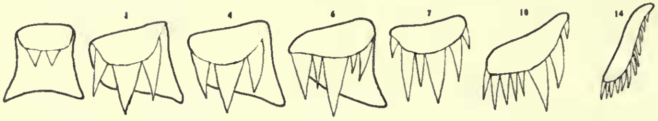
SHELL. All three specimens were large, the biggest was 11·1 mm. long, 4·9 mm. wide, 5·5 mm. aperture length and 2·7 mm. aperture width. The other two specimens were 9·7 mm. and 8·2 mm. long. The body whorl is approximately equal to half the length of the shell and, in the largest specimen the ratio of shell length/aperture length is only 2·02. The shells are thin and smooth on the lower whorls but the apical whorls are ribbed and slightly shouldered.

ANATOMY. All of the specimens were dissected and the penis was unfortunately everted in each. However, there was a considerable proximal dilatation of the penis sheath and all had a long epiphallus. In the two smaller individuals the prostate was about equal to half the total volume of the accessory genital glands, suggesting that both of the specimens were probably only just functionally hermaphrodite and not yet fully developed. The receptaculum seminis was ovoid and the duct was a little shorter than the maximum diameter of the receptaculum (Text-fig. 97). The mantle markings consist of large, irregular but separate black blotches on a pale grey ground with a wide band of darker grey near to the free edge (Text-fig. 98).

RADULA. The radula teeth are similar to those of *B. forskali* with slightly longer mesocones on the laterals. Very small interstitial cusps are present between the endo- and mesocones and between the ecto- and mesocones of all the laterals. The fourth lateral on one side of one of the radulae had an additional endocone. Each row had seven tricuspid laterals and sixteen marginals (Text-fig. 99).

It is interesting that this small sample was the only material of *B. scalaris* found during this investigation and it came from a locality well away from those previously recorded in Angola. The type-locality of the species given by Dunker is the marshy areas around lakes near Benguela. Sowerby gives the locality for *benguelensis* (Pl. 9, figs. 4–6) as Benguela, Egypt, but this almost certainly refers to the small coastal village of Egito near Benguela. Morelet records *scalaris* from stagnant waters near Luanda and from *Lemna*- covered pools in the neighbourhood of Ambriz and gives the type-locality for *canescens* (Pl. 9, figs. 7, 8) as the marshes around the river Bengo near Quicuje (the Bengo flows out between Luanda and Ambriz).





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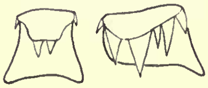

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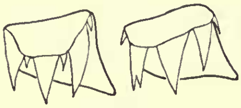

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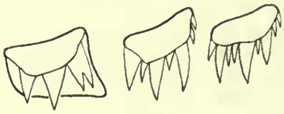

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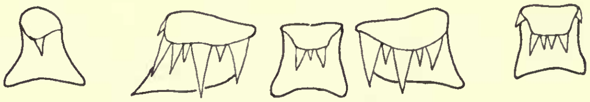

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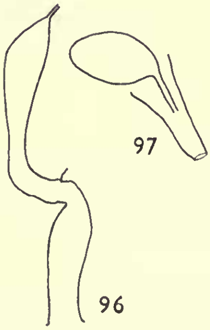

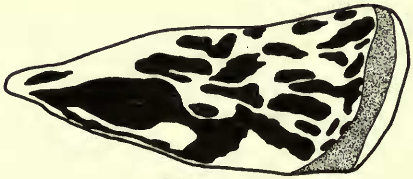

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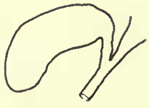

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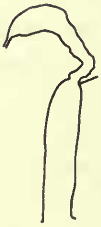

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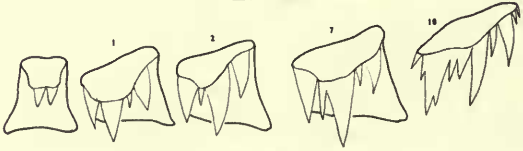

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99

All of these places are in the coastal plain but the sample described here came from the plateau not far from Malange. The range of *scalaris* extends through Central Africa and up into Kenya and Uganda.

The placing of *canescens* in the synonymy of *scalaris* will undoubtedly be questioned by some authorities. Mandahl-Barth (1957b) refers to *canescens* as an extreme form of *forskali* and mentions that the only material which he has seen came from a cattle trough on Lochinvar ranch, Northern Rhodesia. I have been fortunate in having material from this same locality breeding in the laboratory and have been able to study it in considerable detail. The male copulatory organ (Text-fig. 96) is characteristic for *scalaris*, having a wide proximal dilatation of the penis sheath and a very long epiphallus. Although the shells of the majority of the original Rhodesian specimens are completely smooth and lacking either ribs or carination many of the laboratory-bred specimens are clearly ribbed and some have a slight shoulder on the upper whorls. Morelet (1868) described *canescens* as having fine growth lines which appear as weak ribs on the upper whorls of some specimens. He reported that a number of individuals showed marked ribbing and carination of the upper whorls and he suggested that these might be hybrids between *canescens* and another species. Morelet also mentioned that Dunker's definition of *scalaris* was inadequate in that it failed to include some forms with shorter spires and others which are turriculate. A careful examination of the type series of *scalaris* (Pl. 9, figs. 1–3) shows a distinct carination on the apical whorls of two of the three specimens, also quite clearly marked ribs (Pl. 10). There is, therefore, no doubt that *canescens* is a form of *scalaris* and the definition of the species must include the presence of a slight carination and ribs on the upper whorls.

The form referred to under the name *B. scalaris* by Carvalho and Janz (1960) is undoubtedly *B. crystallinus* (Morelet).

Bulinus crystallinus (Morelet)

Physa crystallina Morelet, 1868: p. 89, pl. 9, fig. 4.
Bulinus senegalensis; Janz & Carvalho, 1956.
Phisa sp.; Casaca & Carvalho, 1955.
Bulinus scalaris; Carvalho & Janz, 1960.

MATERIAL. A total of seventeen shells was received from Dr. Morais de Carvalho, all collected in the neighbourhood of Salazar, Cuanza Norte in the Rio Moembege

FIGS. 83–95. *Bulinus forskali*. Figs. 83–90. Male copulatory organs and receptacula of specimens from Lagoa Dalagosa. (83–85) ; Lagoa Panguila. (86) ; Lagoa Quilunda. (87) ; Dondo. (88) ; Laboratory-bred Lagoa Panguila. (89 & 90). Fig. 91. Radula teeth of specimen from Dondo. Fig. 92. Aberrant central and first lateral, Dondo. Fig. 93. Aberrant first and fourth laterals, Lagoa Quilunda. Fig. 94. First, fifth and seventh laterals, Dalagosa. Fig. 95. Three aberrant centrals and two first laterals, Bom Jesus.

FIGS. 96–99. *Bulinus scalaris*. Fig. 96. Male copulatory organ of specimen from Lochinvar Ranch, Southern Rhodesia. Fig. 97. Receptaculum, Quionqua. Fig. 98. Mantle, Quionqua. Fig. 99. Radula teeth, Quionqua. Figs. 100 & 101. *Bulinus crystallinus*, receptaculum and male copulatory organ.

and its tributaries (Rio Camundai, Rio Conda, the irrigation system of a vegetable garden in Salazar and at Quifué on the Moembege above Salazar). September, 1954.

HABITAT. Casaca and Carvalho (1955) mention that in the area around Salazar they found freshwater snails only in the slow-flowing parts of the streams, particularly where the water was dirty and contained rotting banana leaves. Presumably these specimens were found under these conditions.

SHELL (Pl. 11, figs. 4–7). The largest specimen in the sample measured 9·5 mm. long, 4·6 mm. wide, 5·8 mm. aperture length and 2·7 mm. aperture width. The mean length of the sample was 7·4 mm. The body whorl is about two-thirds of the total shell length and the spire is relatively short and pointed. The mean value of the ratio shell-length/aperture length at length 7·5 mm. is extremely low, only 1·67, and the value of the ratio length/aperture width at the same size is also low, 3·43. These two indices express the low spire and relatively great width of the shells, giving them the appearance of belonging to the *truncatus* rather than to the *forskali* species group. The whorls are markedly shouldered and regularly and strongly ribbed. The shells are of a reddish-brown colour.

ANATOMY. Examination of the shells showed that some still contained the dried bodies of the animals. Three of these specimens were carefully cracked and incubated for three days at 35° C. in a 0·5 per cent. solution of tri-basic sodium phosphate (van Cleave and Ross, 1947). This treatment did not restore the animals completely but it enabled some observations of the anatomy to be made. The mantle markings were large, irregular black blotches on a grey ground and the ridges on the underside showed that the material belonged definitely to the *forskali* group. All three of the specimens were fully mature and in one there appeared to have been a regression of the prostate suggesting that the functionally hermaphrodite stage of the sex cycle was passed and that the specimen was effectively female only. The male copulatory organs of two individuals were removed intact. The preputium in both was a little longer than the penis sheath, the proximal dilatation of the sheath was only a little narrower than the diameter of the preputium and the epiphallus was short (Text-fig. 101). The receptaculum seminis was seen intact in one specimen only and it was extremely large and sac-like with a relatively short duct (Text-fig. 100).

RADULA. The radulae of these specimens showed no obvious malformation and the teeth are similar to those of *B. forskali* from Dondo but with seven tricuspid laterals and seventeen to eighteen marginals.

The question of whether *B. crystallinus* is really a distinct species still remains unanswered for other members of the *forskali* group have not been found associated with it and it may be no more than a very extreme local form. It is the only member of the group so far recorded from the escarpment zone (the type locality is also in this zone, in the Golungo Alto district) of Angola and it appears to be confined to this region. Despite intensive searches of the Rio Moembege and its tributaries over a period of three days in late October 1957 I was unable to find even empty shells of this species. Reference to Welwitsch's manuscript notes indicates that the original material was probably collected in February 1855 but collections in the same area were also made in October 1855 and October 1856.

The material described by Carvalho and Janz (1960) as *B. scalaris* is based on material from Salazar, the origin of the present specimens. They describe the shell characters in detail and show graphically how they can be distinguished from *B. forskali*. The copulatory organ which they describe and figure is not unlike that described here but they indicate that there is a long coiled epiphallus like that in *scalaris*. They do note that they also found material in Benguela and this may have been true *scalaris*.

Lymnaea natalensis Krauss

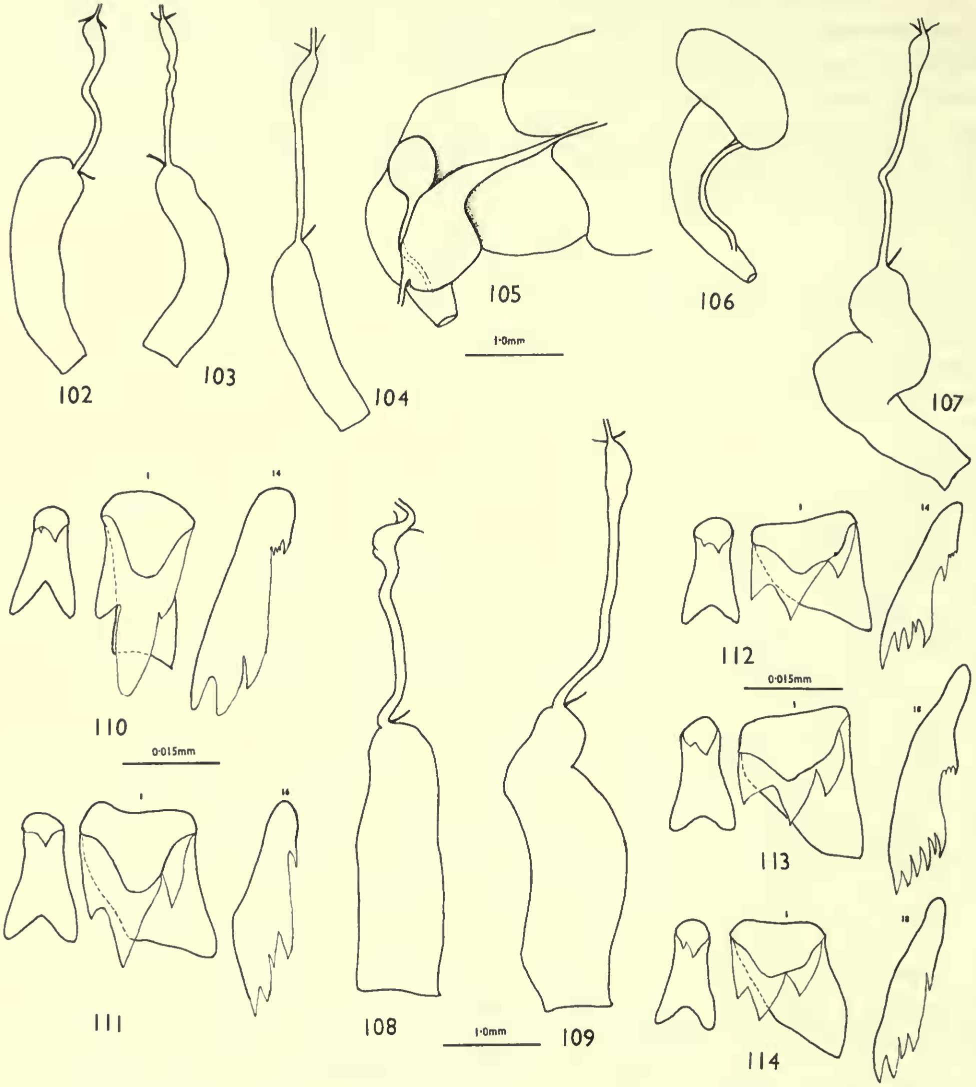
Limnaeus natalensis Krauss, 1848: p. 85, pl. 5, fig. 15.
Limnaeus succinoides Morelet, 1866: p. 161.
Limnaea Bocageana Morelet, 1868: p. 86, pl. 7, fig. 3.
Limnaea Benguelensis Morelet, 1868: p. 86, pl. 6, fig. 4.
Limnaea sordulenta Morelet, 1868: p. 87, pl. 7, fig. 5.
Limnaea orophila Morelet, 1868: p. 87, pl. 7, fig. 4.

MATERIAL

Panguila (*Lagoa*), large lake on banks of Rio Bengo. 43 specimens. 8th November, 1957.
Quequesse (*Lagoa*), grass-choked swamp near Bazabom. 2 specimens. 13th November, 1957.
Tentativa (*Fazenda*), irrigation ditches on sugar-cane plantation and stream carrying effluent from factory. 103 specimens. 8th November, 1957.
Quissol (1), small stream two miles west of Quissol on Malange road. 9 specimens. 24th October, 1957.
Quissol (2), dam in Quastimbala stream. 10 specimens. 24th October, 1957.
Moembege (*Rio*), backwater of stream. 6 specimens. 30th October, 1957.
Cangombe, pools in stream bed. 48 specimens. 21st November, 1957.
Capemba and San José, in shallow seepage water and pools. 51 specimens. 21st November, 1957.
Cassinde Pequeno, in shallow pools in run-off from well. 24 specimens. 21st November, 1957.
Cassinga, backwater of Rio Cului. 3 specimens. 22nd November, 1957.
Cativa, washing place in River Cuango. 11 specimens. 23rd November, 1957.
Catoco, stream near village. 30 specimens. 21st November, 1957.
Cului (*Rio*), bridge on Vila Artur de Paiva-Dongo road. 14 specimens. 23rd November, 1957.
Gunda Vunjanga, deep pool in stream bed. 4 specimens. 22nd November, 1957.
Quesso (1), intake of irrigation system for Granja Administrativa. 6 specimens. 21st November, 1957.
Quesso (2), marshy pools near bank of Rio Cubango. 1 specimen. 21st November, 1957.

Senga, stream through village. 2 specimens. 22nd November, 1957.

Vila Artur de Paiva, ditch carrying run-off from spring in town. 6 specimens. 21st November, 1957.



FIGS. 102–114. *Lymnaea natalensis*. Figs. 102–104. Male copulatory organs, Dongo. Fig. 105. Accessory genital glands showing swollen distal part of prostate, Dongo. Figs. 106 & 107. Receptaculum and male copulatory organ, Quissol (1). Figs. 108 & 109. Male copulatory organs, Fazenda Tentativa. Figs. 110–114. Radula teeth, Lagoa Panguila (110), Fazenda Tentativa (111), Quissol 1 (112), Capembe and San Jose (113) and Dongo (114).

HABITAT. *L. natalensis* is the most widely distributed species found in the present work. It was collected in a wide range of habitats from large lakes to small streams and pools, sometimes in very shallow water, usually on vegetation, either aquatic or emergent but also on mud. Some of the specimens from Lagoa Panguila were found just out of the water, crawling on sheltered parts of the emergent vegetation.

SHELL (Pl. 13, figs. 1–6). Although it is subject to considerable variation in detail the shell of *L. natalensis* is remarkably constant in its general characters. The shape is elongate-ovoid, succineiform and the spire is sharply pointed. The maximum width is just over half the shell length and the aperture length is normally three-quarters of the shell length. There is little microsculpture other than fine growth lines, clean shells have a shiny lustre but this is often obscured by algal growths. The shells are almost colourless, sometimes a very pale light brown ; two of the samples collected in Angola (Capemba and Cassinde Pequeno) show well-marked zebrination with alternating light and dark bands. The columella is slightly twisted and the columellar margin is reflexed so that the umbilicus is closed. The outer lip of the aperture is the most variable character of the shell. It is always thin and sharp and it may curve outwards giving a smoothly ovoid aperture or it may be straight or even slightly incurved giving a rectangular appearance. The angle at which the outer lip meets the body whorl also varies from very acute to almost a right-angle. These characters appear to vary more between populations than within them, thus there is a tendency for the samples from the coastal plain to have the outer lip curved and meeting the body whorl at nearly a right-angle while the specimens from the Malange area also have the right-angled junction with the body-whorl but have the outer lip more flattened and those from the southern plateau region have the outer lip flattened and an acute upper angle.

The following table gives the dimensions in millimetres of some of the larger samples collected :—

Locality	Mean Length (Range in Brackets)	Mean Width	Mean Value l/ml (Range in Brackets)
Panguila	12·0 (4·6–19·2)	7·0	1·39 (1·26–1·62)
Tentativa	12·3 (5·9–18·4)	6·2	1·36 (1·09–1·50)
Cangombe	12·4 (8·6–18·9)	6·3	1·43 (1·20–1·71)
Capemba	10·5 (7·5–17·6)	5·75	1·34 (1·08–1·57)
Catoco	11·8 (7·2–16·5)	6·0	1·42 (1·31–1·57)

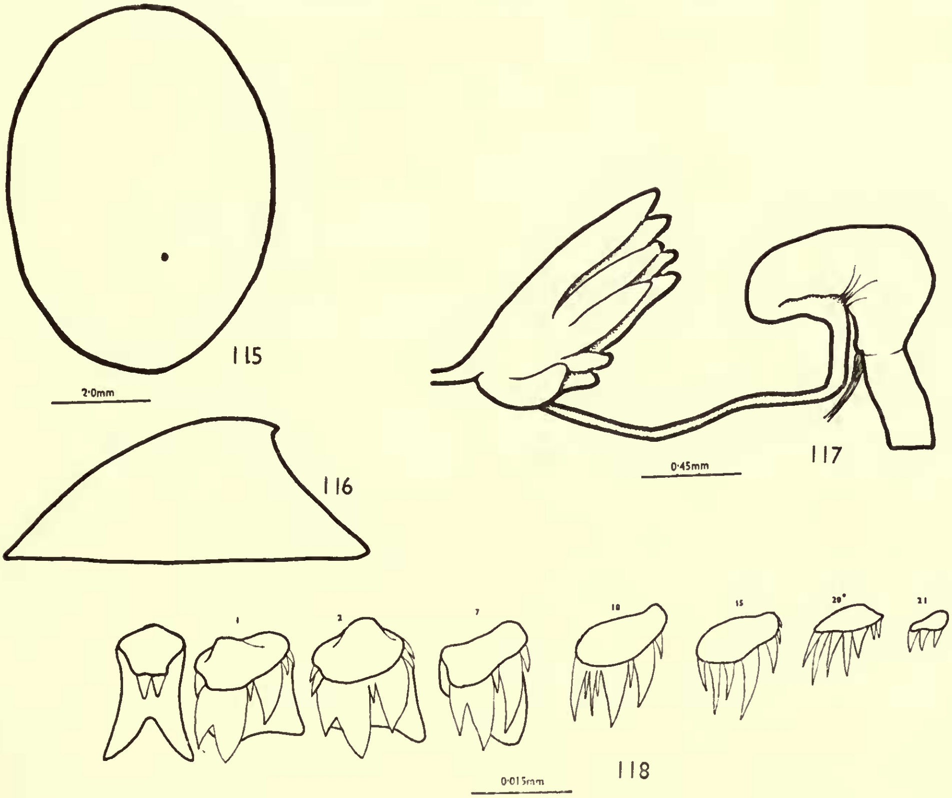
ANATOMY. The colour of the mantle varies considerably between populations. The most usual is a dark sepia ground colour with sparse white and black spots and usually a black bar near the pneumostome. Several of the samples from the southern plateau have the mantle almost uniformly black while others have a light grey ground colour with either black spots and blotches or a black reticulate pattern. Whatever the basic markings of the mantle in any population, it is nearly always lighter in colour in young specimens than adults. The male copulatory organ has the penis sheath and preputium roughly equal in length (Text-figs. 102–104, 107–109), the sheath always very slender with scarcely any proximal dilatation to demarcate it from the vas deferens. There does not appear to be any constancy in the degree of coiling of the penis within the upper part of the sheath. All of the specimens examined had the distal end of the prostate swollen to some extent (Text-fig. 105). The duct of the receptaculum seminis is usually about the same length as the vagina and it is slender (Text-fig. 106) ; in some populations it is longer than in others and this is readily seen during dissection of mature snails for the sperm-filled receptaculum is bright orange in colour and in individuals with a long duct the sac can be seen lying well down on the left side of the body while in those with a shorter duct it is nearer to the mid-line.

A number of the specimens dissected were heavily infected with larval trematodes and in several cases there is little doubt that the fluke concerned was *Fasciola gigantica*.

RADULA. The variation in form of the radula teeth in this species is comparable to that described by Berrie (1960) for *L. peregra* in Sweden. The central tooth is either asymmetrically bicuspid or almost symmetrical with a single cusp. There are usually 8–10 tricuspid laterals in which the endo- and mesocones are almost completely fused. The cusps on these teeth may be relatively short and broad in some populations (Quissol, Dongo, Capemba and San José, Text-figs. 112–114) or longer and more lanceolate (Tentativa, Text-fig. 111) ; those from Panguila (Text-fig. 110) have the tips of the cusps quite blunt and worn-looking even on the new teeth at the back of the radula. The marginals vary widely from a tri-cuspid form with serrations on the outer edge to more delicately comb-like forms with five to eight cusps all of roughly equal size.

L. natalensis was described by Krauss from Natal. Many subsequent authors have described and named other closely related forms from all over tropical Africa but Hubendick (1951) has suggested that there are no anatomical distinctions to support this division and refers them all to the synonymy of *L. natalensis*. Unpublished chromatographic studies in this laboratory have so far confirmed this opinion but Mandahl-Barth (1954) has retained a number of sub-species and states that *L. exserta* from Uganda differs from *natalensis* in that the distal part of its prostate is not dilated. The Lymnaeidae have provided a fruitful source of material for studies in infraspecific variation in several parts of the world and there is little doubt that the forms described from tropical Africa do not merit taxonomic distinction ; Pilsbry and Bequaert (1927) go so far as to say " Few examples of nomenclature so futile and inane can be found, since the variations are far less marked than in any good series of *L. stagnalis* or *auricularia* ". Morelet (1866) named *L. succinoides* (Pl. 12, fig. 4) but in 1868 he altered this to *L. benguelensis* to avoid confusion with *L. succinea* Deshayes, 1834 from India. This action is not justifiable from the nomenclatorial aspect since *succinoides* cannot be regarded as a homonym for *succinea* apart from which *L. succinea* Deshayes is a junior homonym for *succinea* Nilsson 1823. Both *succinoides* (=*benguelensis*) and *orophila* (Pl. 12, fig. 2) were described from the southern area of Benguela, the first from the coastal plain and the other from the Serra de Xella. It is difficult to see how Morelet was able to separate the two species on characters of the shells in the type series. No specimens from either of the type localities of these species were collected during the present expedition but it is interesting to see that the acute upper angle of the aperture and straight peristome are characteristic features of both species as well as of my material from Huila Province. Similarly the original material of *sordulenta* (Pl. 7, fig. 3) from the coastal plain in the neighbourhood of the Rio Dande is reasonably well matched by the large samples recently collected in the same area. *L. bocageana* (Pl. 7, fig. 1) from the Malange area of the plateau is represented only by the two samples from Quissol neither of which have attained anything like the size of the type series (all of which are damaged).

The presence of larval stages of *Fasciola gigantica* in some individuals from all the areas studied indicates that this parasite is extremely widespread in Angola and is likely to be most difficult to control due to the varied ecological tastes of *L. natalensis*.



Figs. 115–118. *Burnupia* sp. cf. *gordonensis*. Fig. 115. Outline of shell, dorsal. Fig. 116. Outline of shell, from left side. Fig. 117. Prostate and male copulatory organ. Fig. 118. Radula teeth.

Burnupia sp. cf. ***gordonensis*** (Melvill and Ponsonby)

Ancylus (*Ferrissia*) *gordonensis* Melvill & Ponsonby, 1903: p. 606, pl. 31, fig. 2.

MATERIAL. About 100 specimens were collected in the Rio Moembege where it passes through the Agricultural Research Station near Salazar, Cuanza Norte. 29th October, 1957.

HABITAT. The stream is moderately fast-flowing between steep banks and heavily shaded by tall bamboo. There is very little emergent vegetation, the specimens were found in considerable numbers in two short stretches of the stream on bracts fallen from the overhanging bamboo and on similar débris. Other snails found were a single *Succinea concisa* on a partially submerged rock and three *Gyraulus costulatus* on tufts of emergent grass a short distance upstream of the *Burnupia* habitat.

SHELL (Pl. 8, figs. 17–19). The sample contained specimens ranging from 9·4 mm. long, 6·6 mm. wide and 3·8 mm. high (this was the largest undamaged specimen but two shells with broken margins were undoubtedly a little bigger) to almost newly-hatched individuals measuring 0·6 mm. long, 0·5 mm. wide and 0·1 mm. high. The majority of the specimens were in the 4·0–6·0 mm. shell length range. The mean dimensions of such a sample are not of any great use but the ratios of shell-width/length and height/length give fairly constant values in all but the youngest specimens. The mean values of these ratios for a sample of twenty specimens are width/length 0·72±0·06 and height/length 0·32±0·02.

The apex of the shell is radially punctate, only slightly displaced to the right of the mid-line and not strongly curved backwards (Text-fig. 115). Both the anterior and left slopes are slightly convex while that on the right is almost straight and the posterior face is concave below the apex but more nearly straight lower down (Text-fig. 116). The sculpture consists of extremely fine wavy radial striae but this is only visible in the younger specimens. In the largest shells no sculpture at all is visible other than poorly defined, slightly irregular concentric growth lines. The colour of the shells is light brown and they are very thin and fragile.

ANATOMY. The gonad consists of a crescentic arrangement of follicles lying near the posterior part of the body beneath the digestive gland. The albumen gland is large, compact and whitish in colour, lying beneath the apex of the shell and above the stomach. The hermaphrodite duct is short with a few seminal vesicles protruding from it. The oviduct is long, thin-walled and very convoluted, it leads into a compact, thick-walled and glandular uterus which is also strongly convoluted. The vagina is short and opens beneath the gill about half-way back on the left side of the body. The receptaculum seminis is club-shaped and the duct is about equal in length to the dilated part. The sperm duct is short and thin-walled, the prostate consists of a fan-shaped arrangement of six or seven long diverticula and three or four short ones opening into an atrium from which the vas deferens runs a short distance in the body wall (Text-fig. 117). Within the head cavity the vas deferens is short and thickened, the male copulatory organ is large and the penis sheath is usually partly evaginated into the preputium which is a little narrower and shorter than the sheath.

Seven out of ten specimens which were dissected were found to be infested with a larval trematode the cercaria of which was furcocercous and, although their state of preservation was poor, they showed some resemblance to *Cercaria oudtshoornia*, described by Porter (1938) from *Burnupia capensis* in Cape Province, South Africa.

RADULA. The radulae of six specimens were examined and proved to be fairly uniform. The median teeth are relatively long, slender and bicuspid. There are seven or eight laterals, basically tricuspid with the endocone and mesocone only partially separated and with very small accessory cusps on the inner margin of the endocone and the outer edge of the ectocone. Most of the laterals have a very small interstitial cusp between the meso- and ectocones. The marginals are about fourteen in number and the outermost ones are simple and comb-like (Text-fig. 118). One of the radulae showed the endo- and mesocones of the first lateral to be fused completely on one side only.

The affinities of this material are not easy to determine and it is with some misgivings that it is referred to *B. gordonensis*. The taxonomy of the African Ancylidae is in a very confused condition as is to be expected in a group with so few clearcut characters. It was hoped that the ratios of shell dimensions might be of some use and the ratios of the twenty-three species of *Burnupia* listed by Walker (1923), Pilsbry and Bequaert (1927) and Mandahl-Barth (1954) were worked out. Of these, sixteen fell within the standard deviation of the width/length ratio of the present sample and only one within the range of the height/length ratio, all of the others (except *B. kempi* (Preston)) being relatively higher. The one species having a similar height/length proportion, *B. capensis* Walker, has a considerably smaller width/length ratio. Comparison with the types or paratypes of a number of species in the collection of the British Museum (Natural History) showed that the majority of the specimens in the sample were more like *B. gordonensis* (Pl. 8, figs. 20–22) than any of the others. The characters of the radula are also more like those described by Walker for *gordonensis* than for any other and include the small accessory cusps on the inner margin of the endocones as well as the interstitial cusp between the meso- and ectocones of the lateral teeth, characters which led Walker to suggest that the radula from which his observations were made was abnormal. Examination of three radulae labelled as *B. capensis gordonensis* in the Gwatkin collection shows them to be apparently similar to the present material but unfortunately the Gwatkin radulae of *Burnupia* are all unstained and therefore not easy to interpret. In the Piele collection there is a radula of a paratype of *B. obliqua* (Krauss) and this is very similar to the present material, but a specimen labelled *B. capensis* has much shorter and more triangular cusps. Walker mentions that some of the samples of *gordonensis* which he examined contained several specimens in which the shell was strongly laterally compressed and one such individual was found in the Angolan sample, in fact it bore a striking similarity to *B. stenochorias* (Melvill and Ponsonby) but the radula is the same as that of the other specimens in the sample and quite unlike that of *stenochorias*. It is perhaps worth mentioning in passing that there is a radula of a paratype of *stenochorias* in the Piele collection and that it differs from the description and figure given by Walker for this species in that the endo- and mesocones of the laterals are not completely fused and, in fact, the endocone is subdivided into two small cusps.

This species appears to be the first ancyclid recorded from Angola (Walker restricted the distribution of *gordonensis* to streams flowing into the ocean between Durban, Natal and Grahamstown, Cape Province) and it is interesting that it was the only one found during the present investigation.

Succinea patentissima Pfeiffer

Succinea patentissima Mencke, Pfeiffer, 1853: p. 52.
Succinea (*Oxyloma*) *patentissima*; Quick, 1936.

MATERIAL

Lalama (*Lagoa*), large lake near Rio Bengo. 1 specimen. 14th November, 1957.
Lumango (*Lagoa*), small lake near Rio Bengo. 12 specimens. 14th November, 1957.
Quequesse (*Lagoa*), grass-choked swamp near Bazabom. 1 specimen. 13th November, 1957.

HABITAT. The three localities in which this species was collected were all on the edge of lakes with a dense fringe of grasses and reeds. The snails were found both in the water and on the stems of plants above the surface.

SHELL (Pl. 14, fig. 6). The shell is little more than a flattened cap which fits over the visceral mass and is not large enough to accommodate the head and foot of the animal. There is a diminutive spire at the apex and this is sharply pointed. The outline of the shell is roughly oblong and the aperture is wide. The columella has a pronounced fold near its upper end but in some individuals this is less well-marked. The shells are thin and translucent and of a pale yellowish-brown colour. The largest specimen examined was 12·6 mm. long and 6·5 mm. wide and the smallest 9·6 mm. long and 5·1 mm. wide.

ANATOMY. The anatomy of this species has been described in detail by Quick (1936). The common genital opening is well forward on the right side of the body and is a simple slit. The general anatomy of the reproductive system and details of the male copulatory organ are shown in Text-figs. 119, 120. The gonad lies near the apex, embedded in the digestive gland and from it arises the hermaphrodite duct, relatively thick and light brown in colour at its proximal end but colourless distally. Just before the hermaphrodite duct enters the albumen gland it gives off two short, blunt unpigmented diverticula which Quick (loc. cit.) describes as seminal vesicles but which Duncan (1961), describing the anatomy of *S. pfeifferi*, suggests are fertilisation sacs. The albumen gland is larger than the gonad and is closely applied to the upper wide loops of the oviduct, embedded in which lies the prostate. The lower part of the oviduct is narrower and sharply coiled and joins imperceptibly into the straight, slightly dilated vagina. The slender receptaculum seminis duct arises from the vagina and runs straight back to the large spherical receptaculum which lies at about the level of the distal part of the albumen gland. The vas deferens runs forward from the prostate almost to the genital atrium and then turns back and lies closely applied to the penis sheath which it enters subterminally at the proximal end. The penis retractor muscle is a prominent feature attached to the extreme end of the sheath. Within the sheath there is a long coiled epiphallus and the penis has a small lateral diverticulum.

RADULA. Each row of teeth is arranged in a shallow M-shape. The tricuspid centrals have a large, dagger-like mesocone with a smaller cusp on either side. The inner laterals are basically bicuspid, apparently consisting of a large mesocone and smaller ectocone and the marginals have five or six cusps including an endocone and subdivided ectocone. Quick noted that the transition from laterals to marginals is not clear in this species since there may be irregular subdivision of the ectocone in the laterals. In this material there are usually five or six bicuspid laterals then about four transitional teeth in which the ectocone is divided and fifty to sixty marginals (Text-fig. 121).

Succinea patentissima appears to be a manuscript name of Mencke and the first published description is that of Pfeiffer. The type locality is given as Port Natal and Connolly (1939) records it also from Zululand, Transvaal, Southern Rhodesia and Lourenzo Marques.

The inclusion of *Succinea* in a work on freshwater gastropods is questionable from the systematic point of view but fully justified ecologically because of the frequency with which these snails are found when searching for purely aquatic forms.

Dr. Quick has been kind enough to examine my material of this and the following species and it is to him that I am indebted for the identifications. The material from Lumango and Quequesse he considers to be typical of the species but the single specimen from Lalama has the columellar fold less well-marked and the distal part of the oviduct is longer.

The only species of *Succinea* previously recorded from Angola is *S. badia* Morelet (Pl. 14, figs. 1–3) collected by Welwitsch from the Islands of Calemba in the Cuanza river to the south-south east of Malange on the plateau.

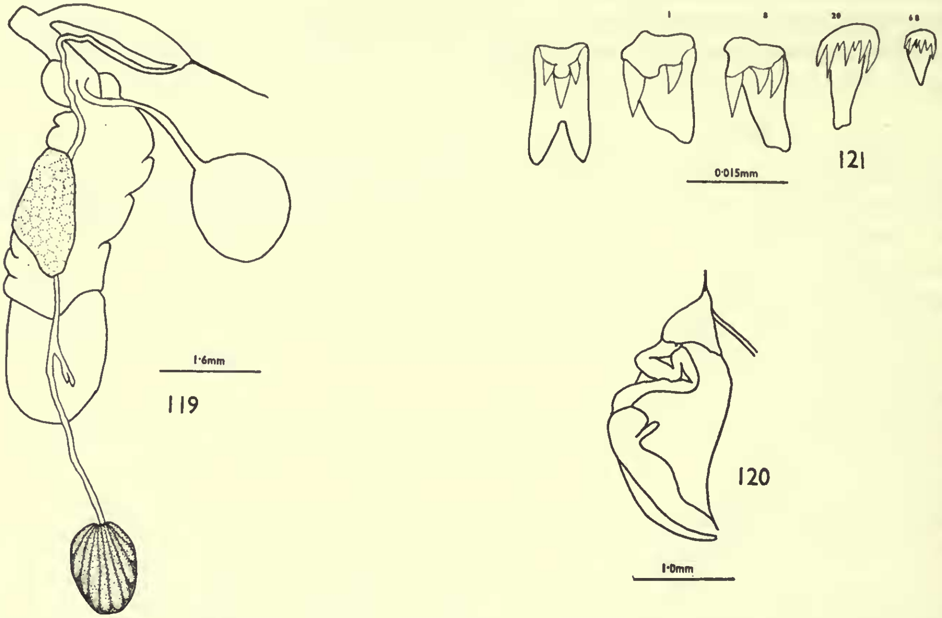
Succinea concisa Morelet

Succinea concisa Morelet, 1848: p. 351.

MATERIAL. *Moembege* (1) (*Rio*), river passing through Agricultural Research Station, Salazar, Cuanza Norte. 1 specimen. 29th October, 1961.

HABITAT. The stream was moderately fast-flowing between steep banks and heavily shaded. The specimen was found on a moss-covered stone sticking out of the water in mid-stream.

SHELL. The specimen was damaged and not well preserved. The shell is better developed than in the preceding species with a more marked but less sharply pointed spire. It is heavily encrusted with mud and detritus, a feature noted by Quick (1936) to be characteristic for the species.



FIGS. 119–121. *Succinea patentissima.* Fig. 119. Whole genital system, ventral view. Fig. 120. Male copulatory organ, penis-sheath opened to show penis. Fig. 121. Radula teeth.

ANATOMY. The state of preservation of the specimen was not sufficiently good to permit a detailed examination of the anatomy but one or two features were observed which differ greatly from *S. patentissima* and which are also described by Quick. There is a dilatation of the hermaphrodite duct which is not seen in *patentissima*. The albumen gland is longer and narrower in *concisa*, the prostate and receptaculum seminis are relatively smaller, the oviduct is less tightly coiled, the vas deferens runs straight to the proximal end of the penis instead of looping forward and the male copulatory organ is small. According to Quick there is no penis sheath in this species but it is not possible to confirm this from the single specimen available. The radula of this specimen was unfortunately lost.

S. concisa (Pl. 14, figs. 4, 5) was originally described from material collected on the banks of the Gaboon river, and Quick's specimens on which his anatomical studies were based came from Sierra Leone, but he also mentions shells from Zanzibar. Pilsbry (1919) quotes Boettger as recording the species from the Congo at Banana Creek.

Lanistes ovum Troschel

Lanistes ovum Peters, Troschel, 1845: p. 215.
Ampullaria ovum; Morelet, 1868.

MATERIAL

Tentativa (*Fazenda*), stream carrying effluent from sugar factory. 7 adult specimens. 8th November, 1957.

Matoz (*Lagoa*), drainage ditch beside small lake on the edge of Fazenda Tentativa. 19 adult, 3 juvenile specimens. 8th November, 1957.

Panguila (*Lagoa*), large lake near mouth of Rio Bengo. 4 adult and 5 juvenile specimens. 8th November, 1957.

Quilunda (*Lagoa*), large lake on the banks of Rio Bengo. 6 adult specimens. 14th November, 1957.

Dalagosa (*Lagoa*), lake on flood plain of Rio Cuanza. 1 adult and 5 juvenile specimens. 13th November, 1961.

HABITAT. This species appears to thrive in still water and seems to be tolerant of fairly polluted conditions. The numbers collected at the localities mentioned above are not an index of their relative abundance since their bulk prevented the accumulation of very large samples.

SHELL (Pl. 15, fig. 4). The spire is well developed and the whorls are gently rounded. The colour varies from dark horn to glossy brown but many specimens from muddy habitats have the shells heavily coated and the colour is completely obscured. The aperture is shaped like an inverted comma, the outer margin is regularly curved and meets the body-whorl at a slightly acute angle and the columella is also gently curved. The columellar margin is very slightly reflexed but all of the specimens have the umbilicus quite open. The only sculpture is of fine growth lines but a few of the smaller adult shells show a very weak malleation of the body whorl. The largest specimen collected has four and a half whorls and is 36 mm. high, 27·5 mm. maximum diameter and 19 mm. aperture height. Mean dimensions of the adult shells from Lagoa Matoz are 23·7 mm. high, 20 mm. maximum diameter and 14 mm. aperture height. Very young juvenile shells are wider than high at the 1–2 whorl stage, colourless and completely transparent.

RADULA. The massive central tooth has a large, pointed median cusp with three smaller cusps on either side. The lateral has a very well developed mesocone, with two smaller outer cusps and a similar-sized endocone and the two marginals are bicuspid with one cusp much larger than the other (Text-fig. 122).

Morelet recorded this species in Welwitsch's collection from Bembo lake on the Dande river, also at Funda, Foto and Moembege. One of the Welwitsch specimens in the British Museum (Natural History) collection (Pl. 15, fig. 1) compares well with my material but is much larger. At five and a half whorls it is 46 mm. high, 40 mm. maximum diameter and 25 mm. aperture height. These dimensions are close to those of another specimen in the collection reputed to be a paratype of *L. ovum* (Pl. 15, fig. 2) originating from the Cumming collection.

My material appears to be very similar to that illustrated by Pilsbry and Bequaert (1927) as *L. adansoni* Kobelt and the measurements agree well. Boettger (1913) considers *adansoni* to be a sub-species of *ovum* but reference to Kobelt's (1911) description suggests that his species (from the Senegambia region) is distinct from *ovum* since its maximum diameter is greater than its height and it is much more widely umbilicate. Kobelt's illustration of *adansoni* looks more like the reputed type specimen (in the British Museum collection) of Morelet's (1860) *L. holostoma*, from Guinea.

L. ovum appears to have great resistance to desiccation. Morelet records that Welwitsch collected blocks of dried mud from the banks of one of the lakes in the coastal plain and these were put in a store room in Luanda and forgotten for two years. When they were eventually placed in water a number of live *Lanistes ovum* emerged.

Lanistes libycus (Morelet)

Ampullaria Libyca Morelet, 1848: p. 28, pl. 3, fig. 9.

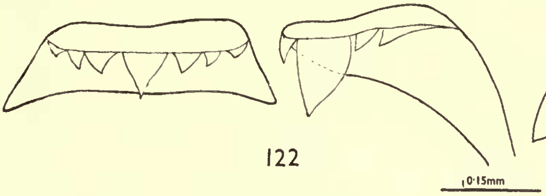
MATERIAL. A single live specimen found in the papyrus swamp fringing the Rio Lucalla above the Duque de Braganza falls. 25th October, 1957.

HABITAT. At the time the specimen was collected the river was low and the living individual was found in a small pool on a mud bank in the papyrus swamp. A number of broken dead shells were seen, suggesting that the snails had been killed by some predator. During the later part of the wet season the river here probably runs very swiftly.

SHELL (Pl. 15, fig. 3). The general shape is globose, sinistral and low-spired, the apex is missing. There are about four whorls and the shell is 27 mm. high, 25·5 mm. wide and the aperture is 19 mm. long. The aperture is roughly oval, slightly narrower above, the outer lip regularly curved and the columella straight. The columellar margin is reflexed, partially closing the umbilicus. The operculum is thin and horny with very fine concentric lines and the nucleus is eccentric, near to the columella. The colour of the shell is drab yellowish-brown with dark brown longitudinal bands which are broader near to the base of the whorl. The internal colour is bluish-white and the bands are purplish-brown colour. The upper part of the whorls is flattened but there is no sharp shoulder angle. There is no carination around the umbilicus. This specimen was a mature female.

RADULA. The radula teeth are very similar to those of *L. ovum* and the only features which appear to be different in *L. libycus* are the reduced outer cusps of the central tooth and the sharply pointed endocones of the laterals (Text-fig. 123). These characters are very variable and if more than one radula of *libycus* were available the range of variation in the two species would probably be found to overlap.

Lanistes libycus (Pl. 16, figs. 5, 6) was described from lakes in Gaboon and has a fairly wide distribution in West Africa. It has not been previously reported from Angola but there is a sample of four shells in the collection of the British Museum (Natural History) from an unspecified locality in the territory. These shells differ from the present specimen in that none has the columellar margin reflexed and all have a trace of an umbilical carination. In their characters the sample shows a range of variation which covers the characters of the single specimen from Duque de Braganza. The type series consists of three adults and one juvenile specimen, all have a relatively well-marked shoulder carination but the angle around the umbilicus is poorly developed in the larger individuals. The type series are all lighter in colour than my Angolan specimen and the band pattern is not so well marked.



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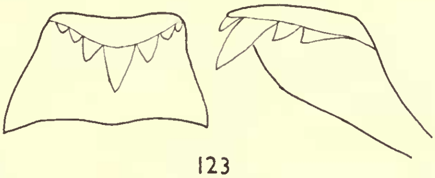

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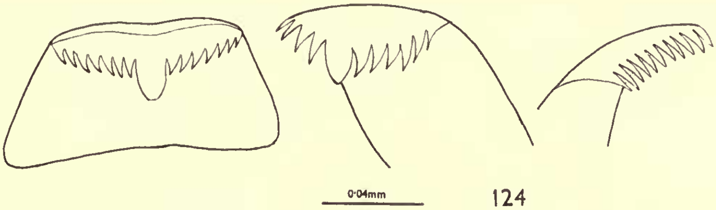

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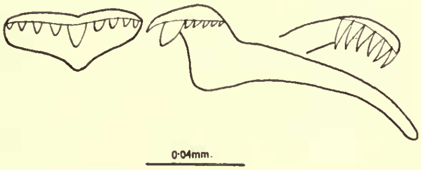

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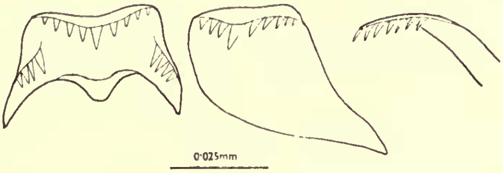

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Fig. 122. *Lanistes ovum* radula teeth. Fig. 123. *Lanistes libycus* radula teeth. Fig. 124. *Bellamya unicolor* radula teeth. Fig. 125. *Melanoides tuberculata* radula teeth. Fig. 126. *Gabbia kisalensis* radula teeth.

Bellamya unicolor (Olivier)

Cyclostoma unicolor Olivier, 1804: p. 39, pl. 31, figs. 9a, 9b.
Viviparus (*Bellamya*) *monardi* Haas, 1934.

MATERIAL. *Cuije* (*Rio*), moderate sized, muddy river, collection made near bridge on Malange-Cangandala road. 6 specimens. 24th October, 1957.

HABITAT. On sticks and debris and on the mud banks of the river which was flowing quite swiftly.

SHELL (Pl. 14, figs. 7, 8). The adult specimens are all very similar in size, one slightly larger than the rest measures 17·5 mm. high, 14·0 mm. wide, 8·5 mm. aperture height and 7·5 mm. aperture width. The colour is drab olive-green and the shell is shiny. The apical whorls have a slight upper carination forming a fairly well defined shoulder and there is also a well-marked peripheral angle which weakens in the largest specimen. The outline of the whorls between the two angles is nearly straight. All of the specimens have the umbilicus open and there is a well-marked umbilical canal. The aperture is nearly circular in older specimens, the columella is gently curved and its margin is not reflexed. The operculum is very thin, corneus and slightly concave. The micro-sculpture consists of fine well-developed spiral lines near the upper part of the whorls and around the umbilicus but the sides of the whorls are smooth. The young, of which eight were found in a single uterus, have the shell quite transparent and the angles most clearly marked and accentuated by the presence of filamentous projections of the periostracum. The spiral sculpture is strongly developed and they are born at about the three whorl stage.

RADULA. The large central tooth has a strong median cusp and seven sharply pointed smaller cusps on either side of it. The lateral and inner marginal teeth are similar to one another with a well-developed middle cusp and five or six curved, sharply pointed smaller ones on either side and the outer marginals are uniformly pectinate (Text-fig. 124).

Bellamya unicolor has a wide distribution in the African continent. Originally described from Egypt, it has been reported by Pilsbry and Bequaert (1927) from several localities in the Congo drainage and the present record appears to be on the extreme edge on the range of the genus (*Bellamya* = *Viviparus*) shown by Pilsbry and Bequaert. However, Haas (1934) described *Viviparus* (*B*) *monardi* from two places in the Cunene system in South Angola, and Connolly (1930), records *B. leopoldvillensis* (Putzeys 1898) from South-west Africa near the Angolan border and remarks that several of the west African species (including *unicolor*) are very similar and may be identical. Mandahl-Barth (1954) has reduced the large number of species described from Lake Victoria to two, *B. unicolor* and *B. jucunda* but he has retained most of the other names as sub-species. No useful purpose would be served by attempting to relate the present small and rather isolated sample with any of these sub-species. Haas' specimens of *B. monardi* from southern Angola are about twice the size of the largest individual in my sample but apart from this there seems to be no justification for regarding them as separate species.

Melanoides tuberculata (O. F. Müller)

Nerita tuberculata O. F. Müller, 1774: p.191.
Melania recticosta E. von Martens, 1882: p. 248.

MATERIAL

Tentativa (*Fazenda*), irrigation ditches of the sugar plantation. About 80 specimens. 8th November, 1957.

Quilunda (*Lagoa*), very common on stones and amongst debris on the beach of this large lake near the Rio Bengo. About 50 specimens. 14th November, 1957.

Quesso (1), intake of the irrigation system for the Granja Administrativa, a single shell collected by Dr. Guedes de Carvalho in October, 1957.

HABITAT. The three localities are all quite different, the irrigation ditches on Fazenda Tentativa had sluggish, muddy water, the intake of the irrigation system at Quesso is fast-flowing and clear and Lagoa Quilunda is a large, open lake with clear water and, at the point where the specimens were collected, the bottom is stony and there is a beach of what appears to be limestone shingle.

SHELL (Pl. 16, figs. 1, 2). The shells of all three lots are superficially different. Those from Fazenda Tentativa have a buff ground-colour with spirally arranged rows of red-brown spots on the lower whorls. These spots are so regularly placed that they also form well-defined transverse rows. The sculpture of the upper whorls consists of two to four spiral ribs but these disappear below the fourth or fifth whorl and the lower part of the shell is almost smooth. The aperture is oval, acutely angled above, the columella is gently curved and light in colour and the columellar margin is reflexed, completely closing the umbilicus. The largest specimen in the sample is 19 mm. high, 8 mm. wide and has an aperture height of 6·5 mm. The sample does not contain many young specimens and the mean shell length is about 14 mm. The specimens from Quilunda are rather smaller and there is a greater number of juveniles in the sample. The shells are extremely light in colour and the suture is shallow. The spots on the lower whorls are either absent or very poorly developed but there is a well-marked dark brown band below the suture and the base of the body whorl has several spiral ribs the presence of which is sometimes accentuated by narrow, light brown bands running between them. The single specimen from Quesso has the apex of the shell missing (this feature is less common in the other two samples than is usual in this species), the ground colour is buff with a pink tinge and the spirally arranged red-brown spots are very well marked on all the whorls. There are well developed spiral ribs on all of the whorls, giving the shell a rougher appearance than any of those in the other samples.

The species is viviparous and possibly parthenogenetic. All of the specimens which were dissected had embryos in the uterus, usually up to ten in a graded series of sizes from five to six whorls downwards but one specimen from Tentativa had over a hundred very small embryos, some without shells. The embryonic shells have the spiral ribs well marked and they also have irregular, coarse transverse ribs. No differences could be found between the embryonic shells of specimens from Quilunda and Tentativa.

RADULA. Radulae from both of the large samples were examined and no differences between them were found. The central tooth is small and roughly triangular with a well developed median cusp and four smaller ones on either side. The laterals have a long tail-like base and seven cusps, the second from the inside edge being considerably larger than the others. The marginals are pectinate with six to eight cusps of equal size (Text-fig. 125).

Melanoides tuberculata is a widespread species whose distribution in Africa has been the source of some controversy. It was originally described from India and Pilsbry and Bequaert (1927) show its range extending from the west coast of North Africa through the Middle East, India, and the Malay Peninsula to southern China and Borneo. In Africa, however, they show it extending as far south as the Transvaal on the eastern side but they claim that it is absent in tropical West Africa and the Congo drainage where it is replaced by a large complex of related species. Connolly (1930) records *M. tuberculata* and *M. victoriae* (Dohrn) from South-west Africa, thus extending the range of *tuberculata* well beyond the south-west limits set by Pilsbry and Bequaert. In 1939 Connolly commented that he only retained the name *victoriae* to distinguish the smoother forms from the more usual tuberculate type and he was obviously not convinced that *victoriae* was a distinct species. Mandahl-Barth (1954) found it necessary to distinguish between three sub-species of *tuberculata* in Uganda, one of which he described as new. There seems to be little justification for the separation of different forms of such a variable species, particularly when, if the animal is parthenogenetic, the characters of the founder member of a population may be of the greatest importance in determining the nature of that population.

The only previous Angolan record probably relating to *M. tuberculata* is von Martens' (1882) species *Melania recticosta* described from the Murie stream, a tributary of the Rio Cuanza on its north bank. It is interesting that Welwitsch did not collect *M. tuberculata* from Lagoa Quilunda because in November 1957 it was undoubtedly the dominant gastropod species in the lake. Fishermen on the lake-shore showed me the stomachs of several freshly-caught catfish which were distended with large numbers of these snails.

Gabbia kisalensis (Pilsbry and Bequaert)

Bulimus (*Gabbia*) *kisalensis* Pilsbry & Bequaert, 1927: p. 216, fig. 17.

MATERIAL. *Cuije* (*Rio*), moderate river, collection made near bridge on Malange-Cangandala road. 16 specimens. 24th October, 1957.

HABITAT. On sticks and debris in the river, collected together with *Bellamya unicolor* and, at the time of collecting, thought to be the young of that species.

SHELL (Pl. 14, fig. 9). Small, globose, pale horn colour, spire short, often missing, aperture almost circular, columella gently curved and outer lip thickened. The shells are perforate but the umbilical slit is narrow. The largest whole specimen collected has three and a half whorls and is 4·6 mm. high, 4·3 mm. wide and the aperture is 2·7 mm. long by 2·2 mm. wide. The mean shell-length of the whole sample is just over 4 mm. and in the smaller specimens (about 3·5 mm. high) the height and width are the same. The operculum fits exactly into the aperture, it is calcareous and has a small spiral nucleus near the centre surrounded by a wide band of concentric growth lines.

ANATOMY. Half of the specimens were dissected and only two males were found. The copulatory organ has a lateral lobe a little longer than the penis but of roughly uniform width. The vas deferens coiled within the head cavity is extremely long.

RADULA.. The central tooth has a sharp, narrow median cusp with four smaller ones on either side and four cusps pointing inward and downward on the sides of the basal plate. The laterals are simple with an off-centre major cusp and about eight others and the marginals have seven equal-sized cusps (Text-fig. 126).

The genus *Gabbia* appears to be mostly confined to eastern Central Africa, particularly in the great lakes region, and the area around Lake Chad. The present record extends the general range by a considerable distance in a south-westerly direction. My material seems to be sufficiently close to *kisalensis* to justify its inclusion in that species despite the greater size of the Angolan form and its greater height/width ratio. From the small specimens in my sample it seems that this ratio definitely increases with growth of the animal and it is probable that in shells as small as those recorded by Pilsbry and Bequaert the relationship between these two dimensions is reversed.

ZOOGEOGRAPHY

The latitudinal range of Angola extends southward from the warm, humid regions of the Congo toward the arid area of the Kalahari desert. Longitudinally the territory can be divided into three topographical regions, in the west a coastal plain of varying width, inland from this a forested escarpment zone, steep and narrow in the south, wider and more gently sloped to the north and an inland plateau extending for many miles to the east, ranging in height between about 3,000 and 5,000 feet. The plateau is divided into northern and southern parts by the Bailundo highlands, an elevated ridge running from south-west to north-east which forms an effective watershed between the major river systems of the Cuanza and Cunene and tends to divide the head-waters of the Zambesi drainage from those of the Congo.

Hall (1960) has given an excellent general description of the topography of the country with particular reference to the importance of the escarpment zone in the distribution of the bird fauna and in another paper the same author (1960a) provides a useful synopsis of the vegetational regions. I have used these two papers together with an unpublished essay on the flora of southern tropical Africa kindly lent to me by Mr. A. W. Exell to supplement my own observations on the areas in which my collections were made. There were four of these areas, the first in the coastal plain around Luanda from the Rio Lifune in the north to the Rio Cuanza in the south, the second in the escarpment zone around Salazar, the third on the plateau around Malange from Duque de Braganza in the north to Pungo Andongo in the south-west and the Rio Cuije in the south-east and the fourth on the southern part of the plateau in the Ganguelas region centred on Vila Artur de Paiva and extending south from Cativa to Cassinga between the Cubangue and Cubango rivers. The accompanying table summarises my own collections on a regional basis and additional information from the literature is included in the account of each area.

		Coastal Plain	Escarpment Zone	Northern Plateau	Southern Plateau
Planorbidae	*Biomphalaria salinarum*			×	
	Biomphalaria pfeifferi				×
	Biomphalaria sp.				×
	Anisus misellus	×		×	
	Gyraulus costulatus		×	×	×
	Lentorbis benguelensis	×			
	Segmentorbis kanisaensis	×			
	Bulinus globosus	×	×	×	
	Bulinus africanus				×
	Bulinus angolensis			×	×
	Bulinus truncatus rohlfsi	×			
	Bulinus forskali	×		×	
	Bulinus scalaris			×	
	Bulinus crystallinus		×		
Lymnaeidae	*Lymnaea natalensis*	×	×	×	×
Ancylidae	*Burnupia gordonensis*		×		
Succineidae	*Succinea patentissima*	×			
	Succinea concisa		×		
Viviparidae	*Bellamya unicolor*			×	
Pilidae	*Lanistes ovum*	×			
	Lanistes libycus			×	
Bithyniidae	*Gabbia kisalensis*			×	
Thiaridae	*Melanoides tuberculata*	×			×

The Coastal Plain

The area is rather flat and featureless apart from the large rivers flowing from east to west which dissect it. The climate of Luanda is defined by Queiroz (1953) as arid tropical and the vegetation in the area visited is mostly of an open grassland type with baobabs near water and a sprinkling of euphorbias elsewhere. Further inland and to the north and south of Luanda there are areas of mixed woodlands and savannah grasslands with acacias, while a strip running south from Benguela is defined as semi-desert and this grades into desert on its south and west sides.

Because of the flat terrain the rivers in this area are slow-moving in the dry season and flood extensively in the rains. There are large depressions on the flood plains of the rivers, some several miles across, which become filled annually and many of them persist throughout the year as large, shallow, muddy lakes, typical examples of which are Lagoa Panguila on the Bengo and Lagoas Dalagosa and Guimbe on the Cuanza. Such lakes usually have a dense cover of waterlily and lotus and provide excellent habitats for mollusc species favouring still water with full sun exposure. It seems probable that the irrigation systems of the Fazenda Tentativa on the Dande and the Fazenda Libongo on the Lifune may have replaced this type of shallow, muddy lake. A second kind of lake is that which does not necessarily have any regular river connection and is deeper than the preceding type, usually without heavy lily-cover but with a thick fringing swamp of papyrus or reeds. Examples of this kind are Lagoas Lalama and Lumango near the Bengo and in these the snail fauna is usually less dense than in the first type but normally includes *Succinea* and a greater variety of small planorbids. A third type of lake is large, open and relatively deep, more or less without lily-cover and with little marginal vegetation. Here there is some wave action and the snails are mostly confined to sheltered places or are found a foot or two below the surface, they may be abundant but the number of species is fewer. Only two lakes of this sort were seen, Cabemba on the Cuanza and Quilunda near the Bengo. During the rainy season there are undoubtedly many smaller temporary water bodies but these were only just appearing towards the end of my work in the area and none were examined.

The dominant pulmonate species found in the Coastal Plain are *Bulinus globosus*, *B. forskali* and *Lymnaea natalensis*. *Anisus misellus* is common and *Segmentorbis kanisaensis* and *Lentorbis benguelensis* are probably widely distributed. *Bulinus truncatus rohlfsi* was found only in Lagoas Panguila and Cabemba, on both occasions on a species of *Ceratophyllum* which was particularly abundant in both of these lakes. *Succinea patentissima* probably occurs wherever the presence of fringing swamps or emergent grass provides a suitable habitat. Although *Bulinus scalaris* was not found in the coastal plain during the present visit it must be common in temporary water bodies during the rains from the frequency with which it was collected by the early explorers. The commonest prosobranch is *Lanistes ovum*, particularly in slow-moving, dirty water and *Melanoides tuberculata* was abundant in the two localities where it was found. The collection in the British Museum (Natural History) contains a sample of *Pila occidentalis* (Mousson) and a series of *Cleopatra bulimoides* (Olivier) both from the Mossamedes area in the south of the coastal plain, also a few shells of *Pachymelania fusca* (Gmelin) from the Rio Tapado near Benguela but none of these species was found around Luanda.

The Escarpment Zone

The description of the escarpment zone given by Hall (1960b) applies mainly to the steep region in the south while the only part which I visited was the area around Salazar where the rise is more gradual. Salazar is at an altitude of about 2,500 feet, to the east the land rises steadily toward Malange but to the west it slopes away more steeply. Queiroz (1953) describes the climate as humid temperate; although this may be technically correct the term temperate is inclined to have a rather different connotation as a general geographical classification and the vegetation in the area is of a degenerate rain-forest type.

Because of the topography most of the streams are fast-flowing and throughout much of their length they are heavily shaded, two physical characteristics which discourage many tropical freshwater snail species. In the immediate area of Salazar however there is some open country and for a short distance the gradient of the Rio Moembege is less steep. In this part of the stream both *Bulinus globosus* and *Lymnaea natalensis* were found and in the same area Dr. Morais de Carvalho collected the specimens of *Bulinus crystallinus* described in this paper. It is significant that the only other definite record for this species (the original material collected by Welwitsch) is also from the escarpment region, a little to the north in the Golungo Alto district. Downstream from Salazar the Moembege becomes more fast-flowing and heavily shaded and it was in a very short stretch of the river under these conditions that *Burnupia sp. cf. gordonensis* was common and two specimens of *Gyraulus costulatus* and one of *Succinea concisa* were found. The river and one of its tributaries were carefully searched for about a kilometre upstream of this point and no further aquatic molluscs were found.

The Northern Plateau

The area around Malange (3,400 feet) is open savannah with Brachystegia woodland. The ground falls slightly towards Duque de Braganza and Pungo Andongo and in both of these areas occasional baobabs are seen near water and the woodland is more dense. There are several moderate-sized rivers in the district (Cuanza, Lucalla, Cole), also smaller rivers and streams. The rivers flow steadily and in places there are sudden drops giving rise to rapids and, in the most extreme case, to the magnificent falls at Duque de Braganza on the Lucalla. In the rivers various prosobranchs are probably common. *Bellamya unicolor* and *Gabbia kisalensis* were found in the Rio Cuije from which von Martens (1882) recorded *Pila ovata ; Lanistes libycus* was collected in the fringing papyrus swamp of the Lucalla. Welwitsch found *Cleopatra bulimoides* in the streams near Pungo Andongo (Pl. 16, figs. 3, 4) but this species was not seen by me. Where the smaller streams have been dammed or the flow is reduced due to widening of the bed a rich pulmonate fauna is present, *Bulinus globosus*, *B. angolensis*, *Biomphalaria salinarum*, *Gyraulus costulatus* and *Lymnaea natalensis* were all found together in the same place. In very stagnant water *Anisus misellus* and *Bulinus forskali* were found and in an apparently temporary shallow, swampy pool *B. scalaris* and *B. globosus* were collected.

Welwitsch obtained *Succinea badia* Morelet on islands in the Rio Cuanza but these were not visited by me and I saw no sign of members of this genus in the area. Despite a careful search of several streams in the neighbourhood of the Pedras Negras, an impressive chain of hills of a dark, conglomerate rock in the area of Pungo Andongo, no freshwater molluscs were found in what often seemed to be almost ideal conditions. The Pedras Negras are rich in minerals particularly manganese, and it is possible that a high concentration of these minerals in the streams makes them unsuitable habitats for snails.

The Southern Plateau

The Ganguelas district in the North-eastern part of Huila Province has a fairly uniform altitude of about 5,000 feet. The country is gently undulating savannah with patches of Brachystegia and mopane woodland, ground orchids are common in damp places and the climate is distinctly cooler than in the three other areas so far described. The principal rivers flow roughly north to south and their tributaries run east-west. In many places it is difficult to decide during the dry season which way the water might flow in the rains because the watersheds are so poorly defined. The rivers on the western side of the district all flow into the Cunene which enters the Atlantic Ocean on the border between Angola and South-west Africa while those on the eastern boundary form part of the Cubango system running south-eastward to drain into the Okavango swamp and Lake Ngami. It is probable that Lake Ngami had relatively recent connections with the Zambesi drainage but Pilsbry and Bequaert's (1927) map indicating the hypothetical extent and distribution of lake and river basins in Africa towards the end of the Pleistocene era also suggests a connection with the Limpopo system.

Because of the terrain in the Ganguelas district the rivers were not fast-flowing at the time of my visit (at the beginning of the rainy season) and many of the smaller tributaries were no more than chains of pools in otherwise practically dry beds. These habitats are ideal for several pulmonate species and in most of them *Bulinus africanus*, *B. angolensis*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* were found, often in considerable numbers, and *Gyraulus costulatus* was usually also present. A second type of habitat in several places (Cassinde Pequeno is the best example) results largely from human activity ; in some of the villages where there is no convenient natural water point a type of open well (caçimba) is dug on a sloping hill-side. Water seeps into the pit and the surplus runs off down the slope where it accumulates in small pools, often only a foot or two across and a few inches deep, and in these *Bulinus africanus* and *Lymnaea natalensis* are common. The irrigation system of the Granja Administrativa near Quesso provides an excellent habitat for *Bulinus africanus*, *Biomphalaria pfeifferi* and *Lymnaea natalensis* all of which were found in the main irrigation furrow. It is interesting that the only indication of the presence of prosobranchs in this area came from a single shell of *Melanoides tuberculata* found at the intake of the irrigation system by Dr. Guedes de Carvalho about a month before my visit. Despite searches in some of the large rivers no other operculates were found but Haas (1934) described *Bellamya monardi* from the Rio Kilui (? =*Cului*) and the Cunene near Mulondo and Connolly (1930) reported *Melanoides victoriae* (=*tuberculata*) from the Cunene as well as *Pila occidentalis* which was originally described from the river by Mousson (1887) and was later reported again by Adensamer (1929). Connolly (1930) also lists a number of prosobranchs collected from the Okavango system (the lower part of the Cubango) by Shortridge and others. Connolly notes that with the exception of *Pila wernei* and *Viviparus leopoldvillensis* all of the gastropods collected by Shortridge were bleached but despite this he believes that they are all still living in the Omuramba-Omatake river which is a tributary of the Okavango.

General Discussion

From this regional account several significant facts concerning the distribution of the freshwater gastropod fauna have emerged. Reference to the table shows that there is only a single species common to all four of the areas visited, namely *Lymnaea natalensis*. This species is widely distributed all over the continent and, although there is considerable local variation, it does not appear to have undergone any distinct speciation. Despite the usually fragile shell and poor ability of the adult snails to withstand desiccation, the species must have characteristics favouring rapid dispersal. The poor differentiation of local forms suggest that *L. natalensis* may be a relatively recent element in the Ethiopian fauna. Apart from *L. natalensis* the only other species which has been found in the coastal plain around Luanda and in the southern plateau region is *Melanoides tuberculata*, the only prosobranch collected in the Ganguelas district despite relatively abundant records of operculates a little further south. Prosobranchs are usually not found in the upland areas of Africa, they are rare on the high veldt of Southern Rhodesia and absent from the highland area of Ethiopia (Wright and Brown, 1962) and it is probable that the Ganguelas district lies near to the altitudinal limits of most prosobranchs in that latitude. The absence of members of the *Bulinus forskali* species group from Ganguelas may be explained in the same way for Connolly (1930) records *B. forskali* from Mafa, north of Ondongua and from Ondongua itself. These local differences in the freshwater faunas of South-west Africa and the Ganguelas region are particularly interesting in the light of Connolly's (1930) comment that there are no species of land snail known to be common to both South-west Africa and Angola.

Two characteristic elements of the plateau fauna both in the north and the south which are missing from the coastal plain are *Bulinus angolensis* and the genus *Biomphalaria*, both are more abundant in the south and are reputed to be common in the central plateau and the Bailundo highlands. *B. angolensis* has already been discussed in the taxonomic section of this paper but *Biomphalaria* is deserving of more attention. Even the limited amount of material of this genus which has been available for study has shown that there is a marked degree of variation between populations in the Angolan region. I have suggested (Wright 1961) that such increased variation in part of the range of a species or species complex may indicate the area in which that species has evolved and I used the complicated situation in the *Bulinus africanus* group in Southern Tanganyika to provide an illustration of this hypothesis. It may be that here in Angola is the original area from which the genus *Biomphalaria* has radiated out.

The distribution of the " small planorbids " shows some apparently characteristic features. *Lentorbis* and *Segmentorbis* were found only in the coastal plain, usually in rather stagnant water, where *Anisus misellus* is also common, but a single sample of this species from the northern plateau indicates its greater range, and if it is the same species as the form recorded under the name *Planorbis gibbonsi* by Connolly (1930), it occurs also in South-west Angola. *Gyraulus costulatus* on the other hand is common in the southern plateau region and has also been found in one locality in the Malange area and one in the escarpment zone, but not together with *A. misellus*. It was suggested in the taxonomic section dealing with *Bulinus africanus* that this species reached southern Angola through the Lake Ngami-Okavango system and it is possible that *Gyraulus costulatus* came the same way and has since spread northward across the Bailundo highlands watershed. *Anisus misellus*, with its close affinities to the west African species referred to *Gyraulus gibbonsi* by Binder (1958), appears to represent (together with *Bulinus truncatus rohlfsi*) a genuinely West African element which has spread southward down the west coast.

The route suggested for the arrival of *Bulinus globosus* in the coastal plain from Tanganyika by way of Northern Rhodesia and Katanga may have been that by which *B. scalaris* and *B. forskali* also entered Angola although *B. forskali* probably arrived earlier than *B. globosus*. *B. crystallinus* may be either a specialised local form evolved in the unfavourable conditions of the forested slopes of the escarpment zone or it may represent a relic of an ancestral form of the *forskali* group whose distribution was wider when the great rain forests covered a much larger area of the continent than they do now. It would be interesting to make a close comparison between *B. crystallinus* and the superficially similar *B. camerunensis* Mandahl-Barth, 1957b, for there is a strong possibility that this species, known only from a crater lake in the Cameroons, may also be an isolated relic of the ancestral form of the *forskali* complex.

To note the presence of certain species in some areas and to suggest how they got there is not enough. It is necessary to try to define the factors which limit the present distribution patterns, if they are in fact limited. The factors are climatic and topographic but it is seldom possible to determine the exact limiting values of any ecological factor because of the interaction between them. In general terms it is probably correct to say that the genus *Biomphalaria* is confined to the Angolan plateau and is absent from the escarpment and coastal plain because the species concerned tend to favour a cooler climate and gently flowing but not turbulent water. The same is true for *Gyraulus costulatus* but in this species the limits of tolerance of water velocity are probably higher, whereas in *Anisus misellus* the opposite conditions seem to be the most favourable. There are undoubtedly many populations of *Burnupia* species in the escarpment region but it is unlikely that they will be found in the coastal plain where the water velocity is less. Harry and Cumbie (1956a/b) have given an excellent illustration of how the effects of topography on stream gradient limit the distribution of *Australorbis glabratus* in Puerto Rico and more recently Scorza et al. (1961) have given a definite limiting value for the factor of water velocity in the distribution of the same species in

Venezuela. The majority of snail habitats in the Angolan coastal plain are in static water while those on the southern plateau are nearly all in water that is either gently flowing throughout the year or periodically flowing, and on the northern plateau there is a mixture of the two general types.

The important climatic factors affecting the distribution of freshwater snails are rainfall and temperature. Rainfall is of direct importance only in that it provides the raw material for bodies of freshwater but it has little or no limiting effect on its own for the porosity of the soil and the topography of the land will determine whether the water is held or not, and the ambient relative humidity will affect evaporation rates and control to some extent the duration of surface water that is retained. Suitable freshwater habitats for snails may be present in areas of low rainfall if the water is provided by rivers (as is the case in the Luanda area of the coastal plain) while steeply sloping areas with high rainfall may not retain enough water to provide habitats. In contrast to rainfall the effects of temperature are direct but not easily measured. It is simple enough to record daily maxima and minima and these are some guide to climate but the upper and lower limiting temperatures governing snail distribution are combined with a time factor. It is possible under laboratory conditions to determine the optimum controlled temperature for breeding of a given snail species and there is a range above and below this optimum within which reproduction can still proceed at a sufficiently high level to maintain the population, provided that the temperature remains within this range for a sufficiently long period. This breeding temperature range is extremely important in determining the distribution of a snail species although there may be cases in which the upper or lower lethal limits of the species' tolerance are involved. Here again there will be a time factor and it is only by experiment that these limits can be worked out. Many African species can withstand temperatures near freezing point for a short period but repeated exposure to such conditions will result in death.

The general picture, then, of the Angolan freshwater gastropod fauna is of two main groups, one composed of species favouring the static water and relatively high temperatures of the coastal plain, the other formed by species preferring the moving waters and lower temperatures of the southern plateau. The elements in each of these groups are probably derived from different geographical origins but the continued separation of the groups is maintained by topographic and climatic differences. In the northern plateau there exist physical conditions within the tolerance of both groups and here the ranges of some of the species overlap. The escarpment fauna is probably rather specialised but where conditions permit there are intrusions from either the coastal plain or the plateau.

ANGOLAN MOLLUSCS OF MEDICAL AND VETERINARY IMPORTANCE

Because this work is connected with a larger study of African molluscs of medical and veterinary importance it is appropriate to include some mention of the economic significance of certain species discussed above as well as the ecology of the transmission cycle of human schistosomiasis in some areas.

Two general reviews have emphasized the widespread incidence of *Schistosoma haematobium* in Angola (Gillet, 1956, Janz and Carvalho, 1956) ; both also mention the scarcity of *Schistosoma mansoni* and the high infection rate in cattle with *S. bovis*.

The earliest quoted record of identified urinary schistosomiasis in Angola is in 1896 and since then records have been gradually accumulating and detailed surveys of a number of areas have been undertaken. Mesquita (1952b) lists the recorded infection rates in twelve localities from all over the territory ; they vary from 16 per cent. at Ambriz to 66 per cent. in Ganguelas and the mean for the twelve sets of figures is just over 40 per cent. Ferreira (1953) in a more general review of disease in Angola noted that the principal foci of urinary schistosomiasis are at Malange, Catete, Caxito, Vila de Ponte and Quilengues, the first in the northern plateau region, the next two on the coastal plain and the other two on the southern plateau. Ferreira also commented on the reduced rate in the central region.

It is fortunate that figures for the incidence of *Schistosoma haematobium* are available for most of the areas in which my collections were made and it is therefore possible to deal with each of the regions in turn.

Coastal Plain. In the Catete area Janz and Carvalho (1956) reported an infection rate of 63·5 per cent. in 1,445 children under fifteen years old and 85·2 per cent. in 889 adults. The rates were equal in children of both sexes and slightly higher in adult men than women. Gillet (loc. cit.) quotes the medical officer of the Fazenda Tentativa sugar plantation as saying that most of the workers on the Fazenda have the infection and Mesquita (1952b) gives the overall infection rate for the Dande area (which includes Fazenda Tentativa) as 61 per cent. These high figures suggest that there is frequent contact with water by the human population and throughout the area *Bulinus globosus* is one of the dominant snail species. The relationship between irrigation and schistosomiasis is too well known for the situation at Fazenda Tentativa to require elaboration. Janz and Carvalho (1956) have suggested that there is a tendency for villages in arid areas to be concentrated near to permanent sources of water and in the Catete region this means the large, shallow lakes near the Cuanza and Bengo rivers. In these lakes there are enormous populations of *Bulinus globosus* and the snails are particularly abundant near to points of human contact. Towards the end of the dry season when the water is low the snail populations are relatively even more dense and it is probably at this time that transmission is at its peak. It is assumed that the form of urinary schistosomiasis in the area is that carried by *Bulinus globosus* but the presence of *B. truncatus rohlfsi* in at least two of the lakes means that conditions for the successful establishment of the " Mediterranean " form of the parasite are available since it has been shown by laboratory experiments (mentioned in the taxonomic section) that this species of snail from Lagoa Cabemba is susceptible to both the Cairo and Khartoum strains of *S. haematobium*.

The Escarpment Zone. Casaca and Carvalho (1955) surveyed the area around Salazar and examined 250 children under fifteen in whom they found an infection rate of 39·7 per cent. in boys and 56·3 per cent. in girls. They also examined 250 adults of which 7·1 per cent. of the men and 34·3 per cent. of the women were passing eggs. The authors searched many streams and rivers in the area and found only snails which they refer to as *Phisa* spp. (probably *B. crystallinus*) except in the Rio Moembege where they found large numbers of *Bulinus globosus* and *Lymnaea natalensis*, also a single *Biomphalaria pfeifferi*. By crushing the snails the authors claim to have found 70 per cent. of the *B. globosus* to be infected with larval schistosomes and 10 per cent. of the " *Phisa* spp." but these figures are exceptionally high and probably include a number of cases of non-pathogenic trematodes. There is no doubt, however, that here the principal intermediate host for *S. haematobium* is *B. globosus* for Casaca and Carvalho found that the species was limited to a certain polluted area of the Rio Moembege and that the overall infection rates in children in sections of the town and its surrounding villages were proportional to their proximity to the heavily snail-infested part of the river. Thus in the district of Alto da Rosa immediately bordering the dirty part of the stream the rate was 85·2 per cent. while in Cassuala and Quifué which are a little further away but draw their water from the same part of the river the rates were 72·7 and 69·2 per cent. respectively. At Quilombo on a clean part of the river downstream from Alto da Rosa the rate was 50 per cent. and in Coqueiros, Camundai and Bandeira on tributaries of the Moembege where only " *Phisa* spp." were found the rates were 44, 24 and 24 per cent. and at Quihanda on a tributary in which no snails were present no cases were found. The evidence suggesting that *Bulinus crystallinus* is transmitting *S. haematobium* is important because it adds another intermediate host to the members of the *forskali* group whose role is so often the subject of discussion. The other point of interest in the observations of Casaca and Carvalho is the limited occurrence of *B. globosus* in the district, confirming that it is not truly a species of the escarpment zone but is only able to exist where changes in stream gradient and openings in the forest provide the necessary conditions of slow-moving water and adequate sunlight. It seems probable that schistosomiasis is of only local importance in the escarpment zone.

The Northern Plateau. Mesquita (1952b) reported a general infection rate of 65 per cent. in Malange and 31 per cent. at Duque de Braganza. Ferreira and Gomes (1959) examined 27,577 urine samples in the Malange district and found an overall rate of 43 per cent. with heavily infected foci at Xa Muteba (5 de Outobro) and Bangale (81 and 70 per cent.) and the lowest incidence at Duque de Braganza with 24 per cent.

Neither of these papers includes information on transmission and my own work in the district was not sufficiently extensive. The rivers are unlikely to be important sources of infection but the temporary pools and small streams, especially where they have been dammed for agriculture or fish-keeping are the most frequent habitats for *Bulinus globosus* and are therefore the potential danger points.

The Southern Plateau. My visit to this area was made possible by the Angolan Medical Services for whom I prepared a brief report on the snail fauna of the Ganguelas district and its probable significance in the transmission of schistosomiasis. Since that report was submitted a urine survey of many of the villages in the area has been carried out (Guedes de Carvalho, 1959) and much of this section is based on my original report and its interpretation in the light of that survey.

Urinary schistosomiasis has been known to occur in Huila Province since 1902 when, according to Janz and Carvalho (1956), the first case was reported by Bernadino Roque. In 1939 a survey of the district around Cuchi was made by Sarmento (1944). Cuchi is in Bié Province but it is particularly relevant to this account because it adjoins Ganguelas on the east side of the Rio Cutato. Sarmento found 60·2 per cent. of the children and 21·5 per cent. of the adults infected and he noted that the incidence was higher in women than men. Cambournac, Gandara and Pena (1955) also surveyed Cuchi and the two districts to the east of it, Menongue and Longa. In Longa the overall incidence was only 3·3 per cent. but in Cuchi and Menongue the rates were much higher (42·3 and 51·6 per cent.). In both areas about half of the children were found to be infected and there was little difference in the rate between the sexes but the percentage of adult females passing eggs was significantly higher than the rate in men. The area is populated largely by two tribes, the Ganguelas and the Quiocos, the Ganguelas are said to be the more primitive of the two and they have a slightly higher infection rate. Two surveys to the west of Ganguelas (Cambournac, Gandara and Casaca, 1956 and Cambournac and Casaca, 1956) provide further information on local infection rates. At Capelongo 13·8 per cent. of 500 people examined were infected, the rate in adult women was again higher than in men, and at Mulondo a 12·9 per cent. rate was detected in 200 children under fifteen years old and 11 per cent. in 800 adults with the rates higher in male children and female adults.

In Guedes de Carvalho's (1959) survey of villages in the Ganguelas district a single urine sample was taken from 35 children between the ages of three and fourteen in each village except where there were less than 35 in a village and in these cases all of the children were examined. In the light of the results from neighbouring districts where a higher rate was found in children than in adults it is likely that the percentage rates given by Carvalho for the villages are greater than the true overall rates. Carvalho gives no figures for the main town of Vila Artur de Paiva but Janz and Carvalho (1956) quote 70 per cent. for a sample of 150 boys and this rate can be considered to be comparable with those given by Carvalho. Only the information relevant to villages whose water supply was examined by me for snails will be considered here.

At Capemba and San José *Bulinus africanus* is common in shallow pools of a hill-side seepage forming the source of a small stream and the infection rates are 57 per cent. for Capemba and 66·6 per cent. for San José. Cassinde Pequeno is close to these two villages and the snail habitat is similar but derived from the excess run-off from a caçimba, here the infection rate is 74·3 per cent. Quesso is the village nearest to the Granja Administrativa and it is probable that the 45·7 per cent. infection rate has its origins in the farm irrigation system although *Bulinus africanus* is common in the marshy ground near to the river bank. Catoco is interesting in that the villagers claim to use the Rio Cubango as their source of water and if this is the case the infection rate in the children should be low because the river does not provide suitable snail habitats. However, the local fear of crocodiles is such that it is most unlikely that they bathe at the point shown to me and a chain of pools in a stream-bed near the village is a much more likely bathing place. These pools are well populated with several snail species including *B. africanus* and the recorded infection incidence of 62·8 per cent. seems to indicate that this is the main transmission point. At Cangombe the heavily snail-infested stream passes through native gardens from which rubbish is dumped into it, and it is also used for washing and bathing. Under these circumstances the 66·6 per cent. infection rate seems low. The stream at Senga passes right beside the village and in it all of the freshwater snail species of the Ganguelas district occur. The stream is used for washing and bathing and the 77·1 per cent. recorded incidence is not surprising. At Gunda Vunjanga the fear of crocodiles prevents the inhabitants from using the nearby Rio Cutato and instead they draw their water from and bathe in a deep pool in a stream bed in which *B. africanus* occurs. In my report I anticipated a high infection rate in this village and this is confirmed by Carvalho's figure of 86·6 per cent. The results of the urine survey at Indungo have provided the greatest surprise, for here the domestic water supply is obtained from seepage pits dug in a wide area of vlie surrounding a small stream bed. No snails were found in either the stream or the pits and the infection rate of 45·7 per cent. suggests that the inhabitants go to some more distant place to bathe.

Two important facts emerge from this survey. The first is the significant part played by the local fear of crocodiles which prevents the inhabitants of many villages from using the relatively snail-free rivers for bathing and causes them to resort to small streams and pools in which *Bulinus africanus* is nearly always present, often in large numbers. Although the only area in which I was aware of this marked fear of crocodiles was in the Ganguelas district, it is undoubtedly widespread ; Livingstone (1857) noted that on the banks of the Lucalla river there were various devices to enable the inhabitants to draw water without coming too close to it themselves. The second important fact in the Ganguelas district is that throughout the area examined the transmission foci are usually well-defined and easy to locate. This should facilitate the problem of control but it is clear that any mollusciciding work will have to be repeated regularly because *B. africanus* is common everywhere in the district and repopulation of treated places is likely to occur rapidly.

The problem of *Schistosoma mansoni* in Angola is exceptionally interesting. Mesquita (1952a) reported two cases in the Malange district, both in individuals who were said not to have left the area but despite repeated surveys for intestinal parasites no other cases were reported until one was diagnosed in Benguela in a native from the Moxico area. As a result of this finding a large survey was carried out in Alto Zambeze (Janz and Carvalho, 1957) and a 1·1 per cent. infection rate was found in over 2,000 individuals examined.

Throughout the plateau region snails of the intermediate host genus *Biomphalaria* are found and it is difficult to believe that they are all resistant to infection with *S. mansoni*. *B. pfeifferi* which is common in Huila Province is certainly known to be a successful host in other parts of Africa and it seems that the only possible explanation is that the parasite has not yet been introduced into the area. With increased movement of Africans as communications in the continent improve it is very likely that intestinal schistosomiasis will eventually become established at least in some parts of the Angolan plateau.

Information about parasites of cattle in Angola is not available apart from Gillet's (loc. cit.) mention of the finding of *Schistosoma bovis* in the mesenteric plexus of eight out of ten cattle from Bom Jesus which were examined in the abattoir at Luanda and Janz and Carvalho's (1956) report of the eggs of *S. bovis* in the faeces of 78·1 per cent. of 258 cattle at Bom Jesus. These last authors also examined the faeces of 33 goats, sheep and pigs in the same area but without success. The cattle ranch at Bom Jesus receives stock from many parts of the territory and the origin of the cases reported is therefore uncertain but it is probable that the parasite is widespread. The intermediate hosts for *S. bovis* are the same as those for *S. haematobium*. The wide distribution and abundance of *Lymnaea natalensis* and the presence of larval forms of the cattle liver fluke *Fasciola gigantica* in many of the specimens examined makes it probable that this parasite is widespread in Angola. The finding of amphistome cercariae in specimens of *Bulinus angolensis* suggests that these flukes too are likely to be widespread at least in the plateau region.

ALPHABETICAL LIST OF COLLECTING PLACES

1. Bom Jesus, Luanda Province. 9° 09′ S., 13° 34′ E. Small lake on the banks of the Rio Cuanza, contained only a few inches of stagnant water when visited on 13th November, 1957. *Anisus misellus, Bulinus globosus, B. forskali.*

2. Cabemba (Lagoa), Luanda Province. 9° 18′ S., 13° 55′ E. Large lake on the flood plain of the Rio Cuanza. The point visited was a muddy sand beach near a fishing settlement. There was emergent grass at both ends of the beach and a floating island of vegetation about half a mile off-shore. Snails were collected on *Ceratophyllum* sp. in about one foot of water off the beach. 14th November, 1957. *Bulinus truncatus rohlfsi* and *B. forskali.*

3. Cabungabunga (Lagoa), Luanda Province. 9° 07′ S., 13° 44′ E. Lake on the flood plain of the Rio Cuanza on the road from Catete to Muxima. Point visited was a large pool on the edge of the main lake, lily-covered and with thick black mud bottom. 13th November, 1957. *Bulinus globosus* and *B. forskali.*

4. Cangombe, Huila Province. 14° 27′ S., 16° 14′ E. Village about four kilometres from Vila Artur de Paiva on Galangue road. Snails collected from a chain of pools in an almost stationary stream passing through native gardens just below the washing place. 21st November, 1957. *Biomphalaria pfeifferi, Gyraulus costulatus, Bulinus africanus, B. angolensis* and *Lymnaea natalensis.*

5. Capembe and San José, Huila Province. 14° 20′ S., 16° 14′ E. Twin villages sharing a water point about eight kilometres from Vila Artur de Paiva on the Galangue road. Water drawn from a seepage ditch cut in the hillside below the villages. The ditch is the beginning of a small stream flowing into the Rio Cubango. 21st November, 1957. *Bulinus africanus* and *Lymnaea natalensis.*

6. Cassinde Pequeno, Huila Province. 14° 22′ S., 16° 17′ E. Village about nine kilometres from Vila Artur de Paiva on Galange road. Water point a half open well (caçimba) on the hillside into which water seeps and the surplus runs off in a trickle forming pools in which snails were common. 21st November, 1957. *Bulinus africanus* and *Lymnaea natalensis*.

7. Cassinga, Huila Province. 15° 08′ S., 16° 05′ E. Village about 90 kilometres south of Vila Artur de Paiva. Waterpoint in a backwater of the Rio Cului, near the ford. Snails scarce and small. 22nd November, 1957. *Bulinus africanus* and *Lymnaea natalensis*.

8. Cativa, Huila Province. 14° 10′ S., 16° 12′ E. Village about 45 kilometres north of Vila Artur de Paiva on track leading from Galangue road. Water point in Rio Cuando, slow moving tributary of Rio Cubango. Snails not numerous, but present on broad-leaved aquatic plants. 23rd November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus* and *Lymnaea natalensis*.

9. Catoco, Huila Province. 14° 36′ S., 16° 24′ E. Village about 12 kilometres south south-east of Vila Artur de Paiva, not in the position shown on the 1 : 1,500,000 Carta de Angola (1935). Water point reputed to be in Rio Cubango but this is unlikely to be a bathing place because of the fear of crocodiles. In a shallow valley on the Vila Artur de Paiva side of the village there were pools in a stream bed and snails were plentiful here. 21st November, 1957. *Bulinus africanus*, *B. angolensis* and *Lymnaea natalensis*.

10. Cuije (Rio), Malange Province. 9° 35′ S., 16° 25′ E. Moderate sized river, very muddy and at low water when visited, 24th October, 1957, tributary of the Rio Cuanza. Searched on both banks for several hundred yards on either side of the bridge on the Malange-Cangandala road, also pools on the flood plain on the south bank. *Bellamya unicolor* and *Gabbia kisalensis* in the river and *Bulinus forskali* in a pool on the flood plain.

11. Cului (Rio), Huila Province. 14° 30′ S., 16° 01′ E. Almost stagnant pools in the river bed with heavy lily cover and emergent vegetation. Point visited beside bridge on Vila Artur de Paiva-Dongo road. 23rd November, 1957. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Bulinus africanus*, *B. angolensis* and *Lymnae natalensis*.

12. Dalagosa (Lagoa), Luanda Province. 9° 07′ S., 13° 44′ E. Lake near the village of Bazabom, about 18 kilometres from Catete on Muxima road, on flood plain of Rio Cuanza. Water very low and lake greatly contracted at the time of the visit. 13th November, 1957. Thick black mud bottom, some lily cover and *Ceratophyllum* sp. Snails abundant. *Bulinus globosus*, *B. forskali* and *Lanistes ovum*.

13. Dondo, Cuanza Norte Province. 9° 38′ S., 14° 25′ E. Material collected by Dr. Morias de Carvalho from the Rio Mucoso. 3rd July, 1957. *Anisus misellus* and *Bulinus forskali*.

14. Dongo, Huila Province. 14° 36′ S., 15° 48′ E. Village about 80 kilometres west of Vila Artur de Paiva. Water point in the Rio Cubangue which, when visited

was shallow and slow-flowing with large pools on the bank. 23rd November, 1957. *Biomphalaria pfeifferi, Gyraulus costulatus, Bulinus africanus, B. angolensis* and *Lymnaea natalensis.*

15. Guimbe (Lagoa), Luanda Province. 9° 10′ S., 13° 40′ E. Large lake near Rio Cuanza, shallow, extensive lily cover and many water birds. 13th November, 1957. *Bulinus globosus* and *B. forskali.*

16. Gunda Vunjanga, Huila Province. 14° 39′ S., 16° 27′ E. Village about 15 kilometres due east of Vila Artur de Paiva. Water point in deep, lily-covered pool in a stream bed. 22nd November, 1957. *Gyraulus costulatus, Bulinus africanus* and *Lymnaea natalensis.*

17. Indungo, Huila Province. 14° 48′ S., 16° 17′ E. Village about 40 kilometres south of Vila Artur de Paiva. Water point consists of a series of seepage pits dug in a meadow. No snails found. 22nd November, 1957.

18. Lalama (Lagoa), Luanda Province. 8° 57′ S., 13° 42′ E. Reed-fringed lake near the Rio Calucala. 14th November, 1957. *Succinea patentissima, Anisus misellus, Lentorbis benguelensis, Segmentorbis kanisaensis, Bulinus globosus, B. forskali* and *Lanistes ovum.*

19. Libongo (Fazenda), Luanda Province. 8° 24′ S., 13° 24′ E. Oil palm plantation near the mouth of the Rio Lifune. Irrigation ditches contained few snails but these exceptionally large. 9th November, 1957. *Bulinus globosus.*

20. Lucala (Rio), Malange Province. 9° 04′ S., 16° 11′ E. Large river, water low, thick fringing papyrus swamp but main channel fast flowing, point visited just above the Duque de Braganza falls. Pools on mud banks in papyrus swamp examined. 25th October, 1957. *Lanistes libycus.*

21. Lumango (Lagoa), Luanda Province. 8° 52′ S., 13° 38′ E. Reed-fringed lake near the Rio Bengo. Marginal vegetation too dense for direct approach to open water. Snails collected in gap in reeds where fishing canoes are drawn up. 14th November, 1957. *Succinea patentissima, Bulinus globosus* and *B. forskali.*

22. Matoz (Lagoa), Luanda Province. 8° 32′ S., 13° 34′ E. Small lake on the north side of the Fazenda Tentativa, near the Caxito-Ambriz road. The lake is reputed to harbour an aggressive crocodile and collecting was confined to a drainage ditch beside it. 8th November, 1957. *Bulinus globosus, B. forskali* and *Lanistes ovum.*

23. Moembege (Rio), Cuanza Norte Province. 9° 20′ S., 14° 52′ E. Moderate stream passing through agricultural research station near Salazar. The stream was examined for over a mile of its length but snails were found only in a relatively short stretch near the main buildings. At this point the banks are steep, the water is swift and shaded by heavy growths of bamboo. 29th October, 1957. *Succinea concisa, Gyraulus costulatus* and *Burnupia* sp. (c.f. *gordonensis*).

24. Moembege (Rio), (2), 9° 18′ S., 14° 54′ E. The stream is similar to the descriptions above but much less shaded for most of its length. It was examined from a point about a mile up-stream of Salazar to just below the town and snails were found in a small backwater, also at the washing place in the town. 30th October, 1957. *Bulinus globosus* and *Lymnaea natalensis.* (Dr. Morais de Carvalho

collected the material of *Bulinus crystallinus* described in this paper from the Moembege and its tributaries in September, 1954).

25. Panguila (Lagoa), Luanda Province. 8° 42′ S., 13° 27′ E. Large lake near the mouth of the Rio Bengo, close to the sea. Three places examined on two successive days (8th and 9th November, 1957), the first was near the bridge on the Luanda-Caxito road, the second was a pool on the edge of the lake near the road and the third point was at the north-west corner of the lake. There is emergent grass all along the west shore and considerable lily-cover on the lake itself. *Anisus misellus, Lentorbis benguelensis, Bulinus globosus, B. truncatus rohlfsi, B. forskali, Lymnaea natalensis* and *Lanistes ovum.*

26. Quequesse (Lagoa), Luanda Province. 9° 07′ S., 13° 44′ E. Grass-choked swampy lake near the village of Bazabom on the Catete-Muxima road. 13th November, 1957. *Succinea patentissima, Anisus misellus, Segmentorbis kanisaensis, Bulinus globosus* and *Lymnaea natalensis.*

27. Quesso (1), Huila Province. 14° 22′ S., 16° 22′ E. Village about seven kilometres north of Vila Artur de Paiva, near intake of the irrigation system of the Granja Administrativa from the Rio Cubango. Dr. Guedes de Carvalho had shells of *Biomphalaria pfeifferi, Bulinus africanus, Lymnaea natalensis* and a single *Melanoides tuberculata* collected here in October but no snails were found in the same place on 21st November, 1957. Further down the irrigation system the first three species were all found but there was no sign of further *Melanoides.*

28. Quesso (2), Huila Province. 14° 22′ S., 16° 22′ E. Washing place for the village is said to be in the Rio Cubango but this seems a little unlikely. No snails were found in the river itself but in a marsh behind the river bank *Bulinus africanus* was common.

29. Quifangondo, Luanda Province. 8° 44′ S., 13° 27′ E. Floating marsh on the banks of the Rio Bengo near to the village. 16th November, 1957. *Anisus misellus* and *Lentorbis benguelensis.*

30. Quilunda (Lagoa), Luanda Province. 8° 50′ S., 13° 36′ E. Large lake on the banks of Rio Bengo. Point visited at east end of lake near Cabire. Open beach of limestone (?) shingle with few marginal bushes and some emergent grasses. Water open, no lily cover, clean stone bottom. Snails were found among the emergent vegetation and damp flotsam on the beach, the prosobranchs were also crawling on stones at least three to four feet deep. Fishermen on the beach showed me the stomachs of fish packed with *Melanoides.* 14th November, 1957. *Bulinus globosus, Bulinus forskali, Lanistes ovum* and *Melanoides tuberculata.*

31. Quionqua (1), Malange Province. 9° 10′ S., 16° 12′ E. Marshy roadside pool about two kilometres north of village on road to Duque de Braganza falls. 15th October, 1957. *Bulinus globosus* and *Bulinus scalaris.*

32. Quionqua (2), Malange Province. 9° 12′ S., 16° 12′ E. Small pool about three feet deep, stagnant and foul with thick mud and marsh gas. Snails on emergent grass. 25th October, 1957. *Anisus misellus* and *Bulinus forskali.*

33. Quissol (1), Malange Province. 9° 35′ S., 16° 28′ E. Small stream crossing

the Malange-Nova Gaia road about five kilometres west of Fazenda Quissol. Water shallow, few aquatic plants. 24th October, 1957. *Lymnaea natalensis.*

34. Quissol (2), Malange Province. 9° 35′ S., 16° 30′ E. Quastimbala stream on edge of Fazenda Quissol. The stream has been dammed to form a pond beside the road. The water is almost still, there is a little lily cover, some reeds and marginal emergent vegetation. 24th October, 1957. *Biomphalaria salinarum, Gyraulus costulatus, Bulinus globosus, B. angolensis* and *Lymnaea natalensis.*

35. Senga, Huila Province. 14° 30′ S., 16° 21′ E. Village about fourteen kilometres east-south-east of Vila Artur de Paiva. The water point is in a stream (possibly the same as that near Catoco), the water was gently flowing and there was a good deal of aquatic vegetation. 22nd November, 1957. *Biomphalaria* sp., *Gyraulus costulatus, Bulinus africanus, B. angolensis* and *Lymnaea natalensis.*

36. Tentativa (Fazenda), Luanda Province. 8° 34′ S., 13° 35′ E. Irrigation system of sugar cane plantation and stream carrying effluent from sugar factory. 8th November, 1957. *Bulinus globosus, Lymnaea natalensis, Lanistes ovum* and *Melanoides tuberculata* (irrigation ditches only).

37. Vila Artur de Paiva, Huila Province. 14° 28′ S., 16° 20′ E. Also known as Vila da Ponte. Main town of Ganguelas District. Water source is a spring near the hospital. The spring itself is covered with a concrete housing but the surplus water runs off down a ditch towards the Rio Cubango. 21st November, 1957. *Biomphalaria pfeifferi, Bulinus africanus* and *Lymnaea natalensis.*

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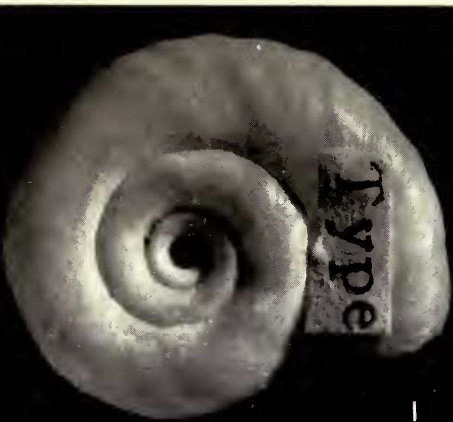
BRITISH MUSEU

PLATE 1

FIGS. 1–6. *Biomphalaria salinarum*, syntypes, B.M. (N.H.) coll. no. 93.2.4.587–9.
FIGS. 7, 8. *B. salinarum*, Quissol, Malange.
FIGS. 9, 10. *Biomphalaria* sp., Senga, Huila.

All figures are × 4 except where stated otherwise.



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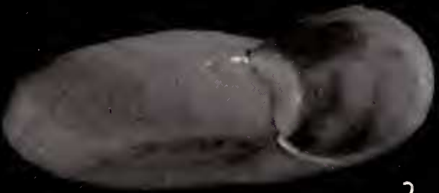

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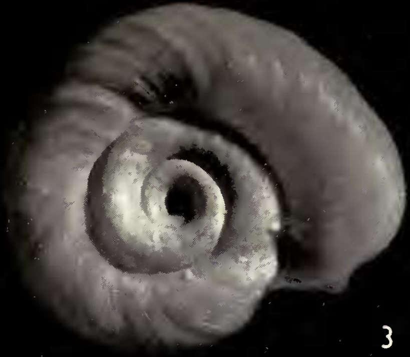

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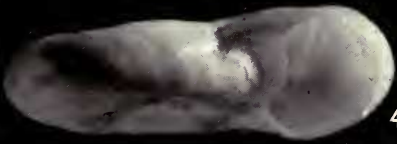

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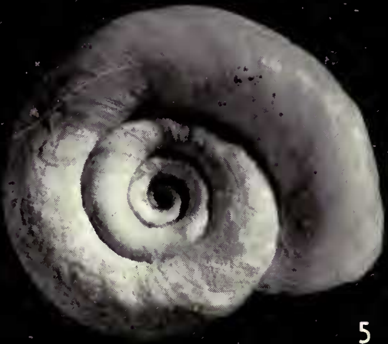

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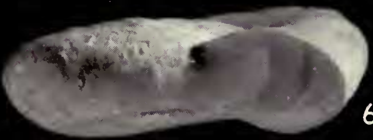

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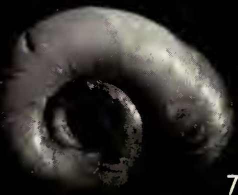

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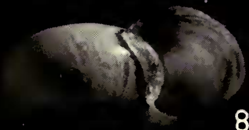

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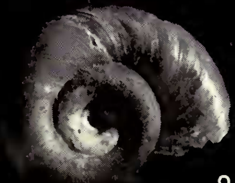

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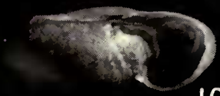

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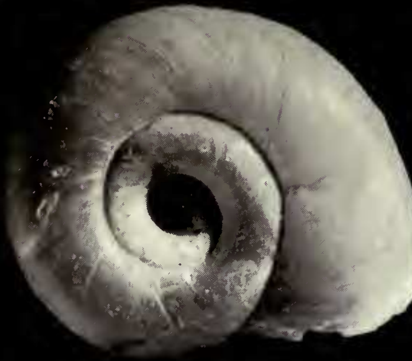
PLATE 2

FIGS. 1, 2. *Biomphalaria* sp., Nova Lisboa.
FIGS. 3, 4. *B. pfeifferi*, Cangombe, Huila.
FIGS. 5, 6. *B. pfeifferi*, Cativa, Huila.
FIGS. 7, 8. *B. pfeifferi*, Vila Artur de Paiva, Huila.
FIGS. 9, 10. *B. pfeifferi*, Dongo, Huila.
FIGS. 11, 12. *B. pfeifferi*, Rio Cului, Huila.
FIGS. 13, 14. *B. pfeifferi*, Quesso, Huila.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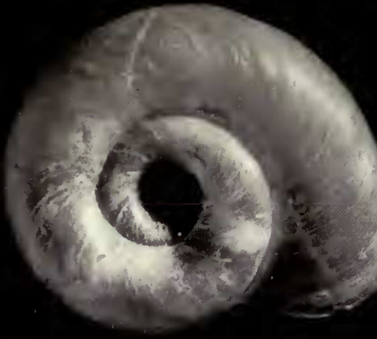
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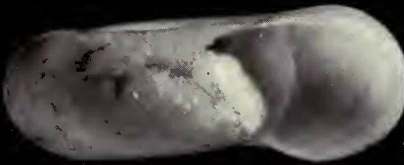
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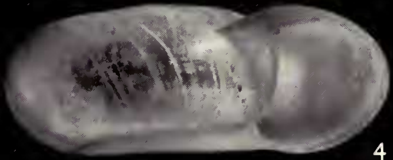
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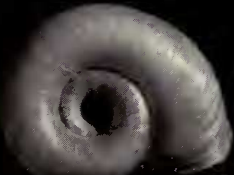
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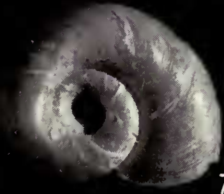
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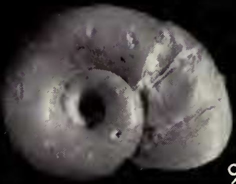
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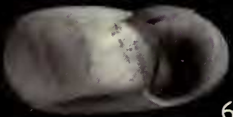
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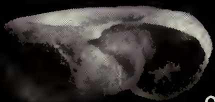
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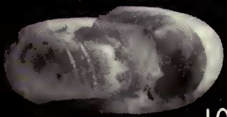
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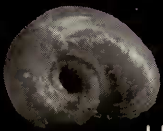
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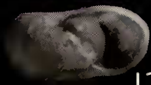
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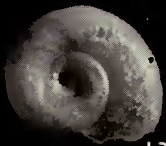
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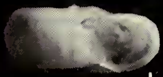
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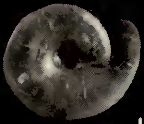
PLATE 3

FIGS. 1, 2. *Lentorbis junodi*, paratype, showing basal lamella. B.M. (N.H.) coll. no. 1937.12.30.8802.
FIGS. 3, 4. *L. junodi*, holotype, B.M. (N.H.) coll. no. 1937.12.30.8801.
FIGS. 5–10. *L. benguelensis*, possible syntypes from Berlin Museum (× 5).
FIGS. 11, 12. *Segmentorbis kanisaensis*, holotype, B.M. (N.H.) coll. no. 1923.6.8.1224.
FIGS. 13, 14. *S. kanisaensis*, paratype, B.M. (N.H.) coll. no. 1923.6.8.1925.
FIGS. 15, 16. *Lentorbis benguelensis* Lagoa Lalama, Luanda.
FIGS. 17, 18. *Segmentorbis kanisaensis* Lagoa Lalama, Luanda.
FIGS. 19–24. *Anisus misellus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.590–4.
FIGS. 25, 26. *Anisus misellus*, Quifangondo, Luanda.
FIGS. 27, 28. *Gyraulus costulatus*, Rio Moembege, Cuanza Norte.
FIGS. 29, 30. *G. costulatus*, Rio Cului, Huila.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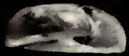
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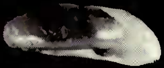
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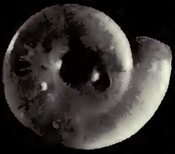
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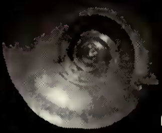
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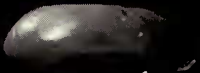
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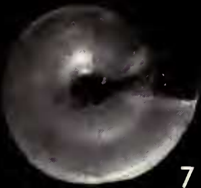
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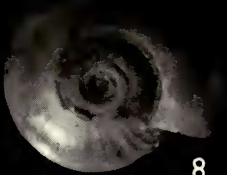
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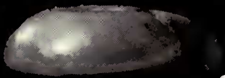
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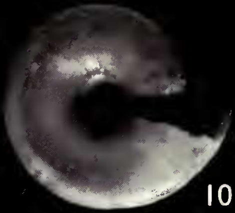
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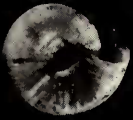
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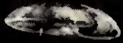
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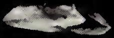
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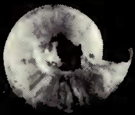
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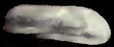
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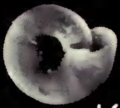
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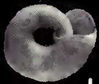
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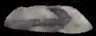
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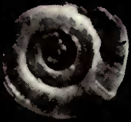
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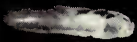
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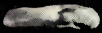
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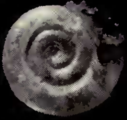
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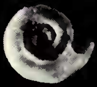
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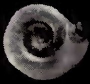
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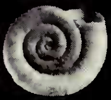
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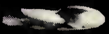
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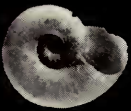
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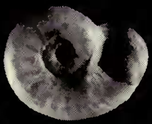
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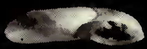
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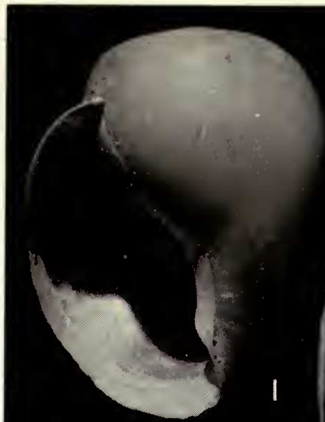
PLATE 4

FIG. 1. *Bulinus globosus*, Lagoa Matoz, Luanda.
FIG. 2. *Bulinus globosus*, Fazenda Libongo, Luanda.
FIG. 3. *Bulinus globosus*, Fazenda Tentativa, Luanda.
FIG. 4. *Bulinus globosus*, Lagoa Dalagosa, Luanda.
FIG. 5. *Bulinus globosus*, Lagoa Quilunda, Luanda.
FIG. 6. *Bulinus africanus*, Cassinde Pequeno, Huila.
FIG. 7. *Bulinus africanus*, Cangombe, Huila.
FIG. 8. *Bulinus africanus*, Quesso, Huila.



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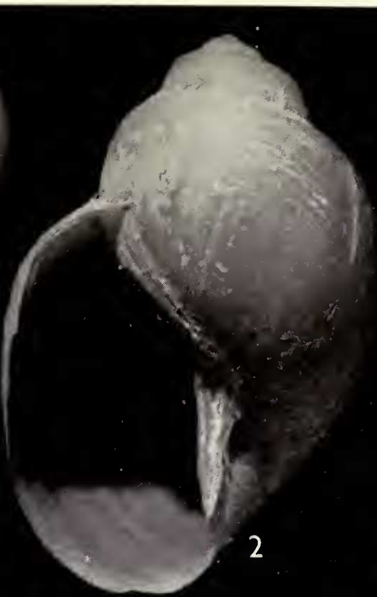

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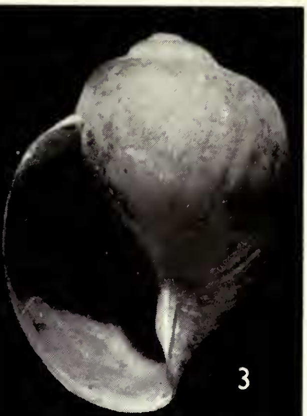

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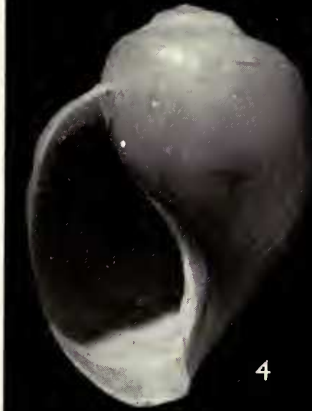

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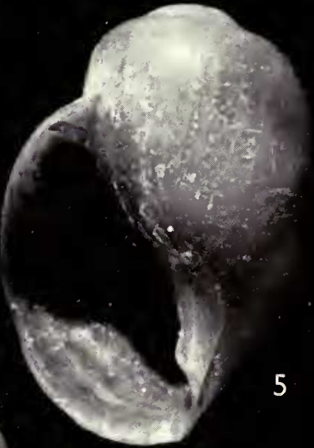

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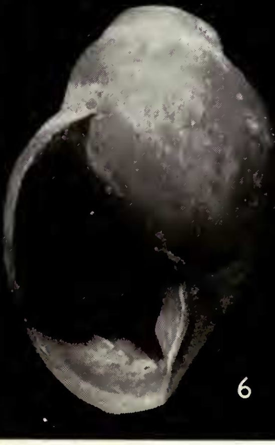

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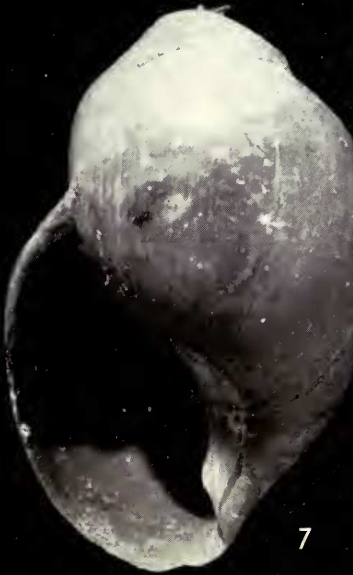

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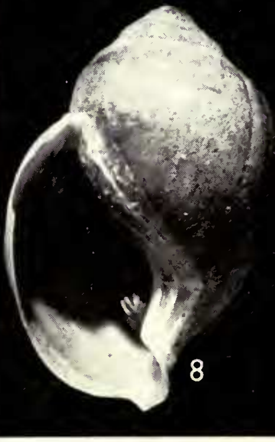

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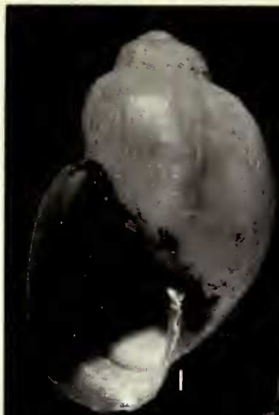
PLATE 5

Fig. 1. *Bulinus angolensis*, Cangombe, Huila.
Fig. 2. *B. angolensis*, Rio Cului, Huila.
Fig. 3. *B. angolensis*, Catoco, Huila.
Fig. 4. *B. angolensis*, Quissol, Malange.
Fig. 5. *B. angolensis*, Dongo, Huila.
Fig. 6. *B. globosus*, holotype, B.M. (N.H.) coll. no. 93.2.4.681.
Fig. 7. *B. globosus*, paratype, B.M. (N.H.) coll. no. 93.2.4.682.



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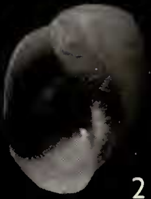

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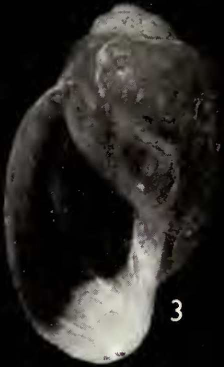

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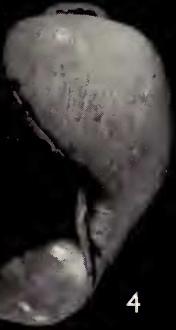

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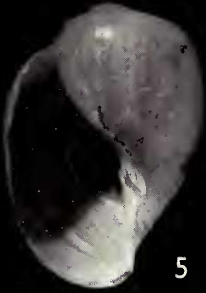

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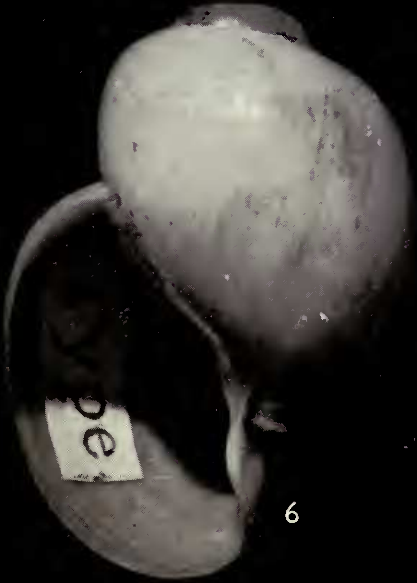

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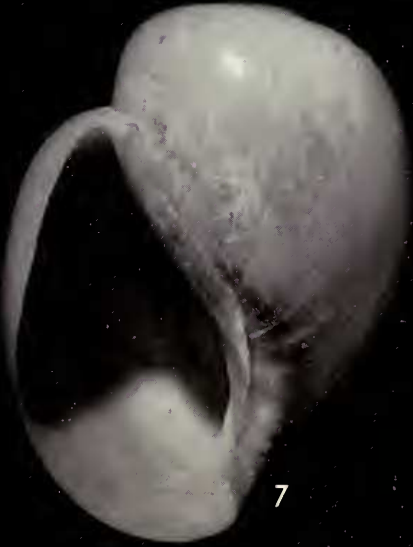

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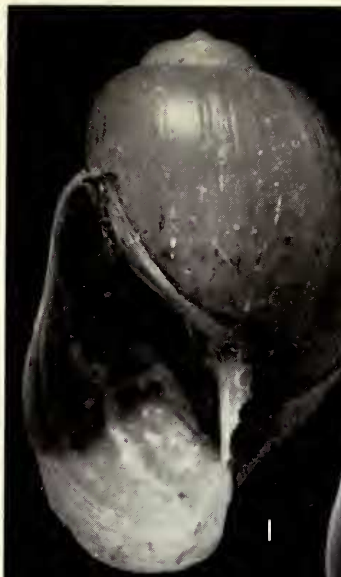
PLATE 6

Bulinus angolensis

FIGS. 1–3. *B. welwitschi*, syntypes, B.M. (N.H.) coll. no. 93.2.4.615–17.
FIGS. 4, 5. *B. angolensis*, syntypes, B.M. (N.H.) coll. no. 93.2.4.618–19.



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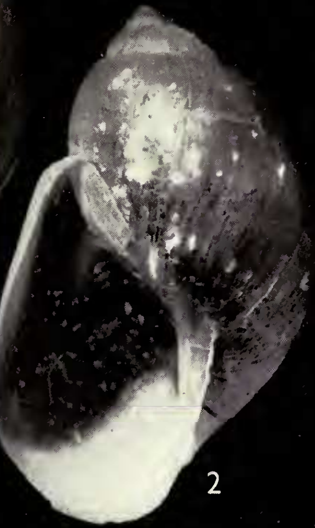

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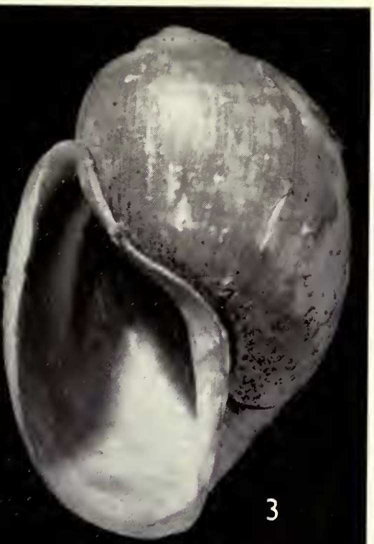

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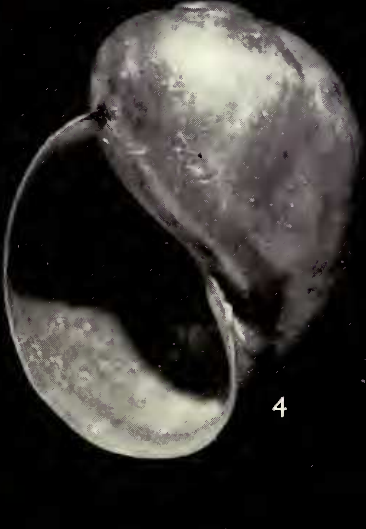

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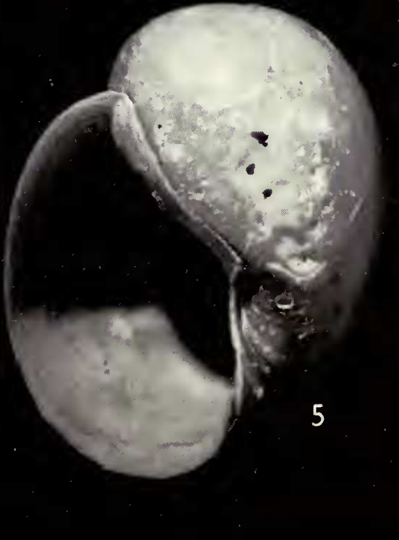

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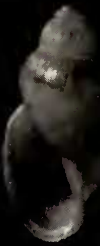
PLATE 7

Bulinus forskali.

Figs. 1–3. *B. schmidti*, syntypes, Berlin Museum.
Figs. 4, 5. *B. capillacea*, syntypes, B.M. (N.H.) coll. no. 93.2.4.654–5.
Figs. 6–9. *B. apiculata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.647–50.
Fig. 10. *B. turriculata*, holotype, B.M. (N.H.) coll. no. 93.2.4.505.
Figs. 11–14. *B. clavulata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.643–6.
Figs. 15–17. *B. semiplicata*, syntypes, B.M. (N.H.) coll. no. 93.2.4.621–3.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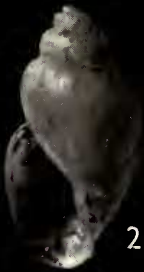
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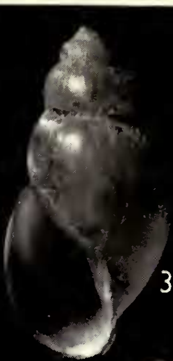
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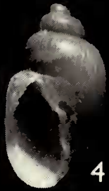
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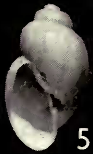
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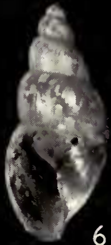
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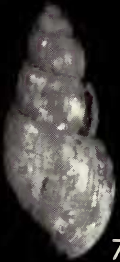
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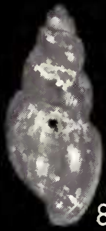
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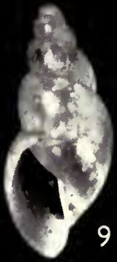
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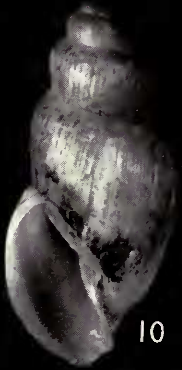
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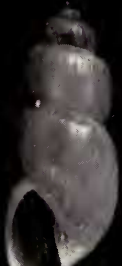
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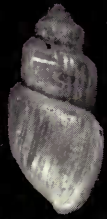
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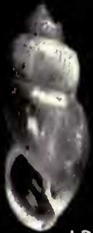
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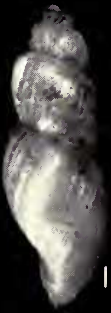
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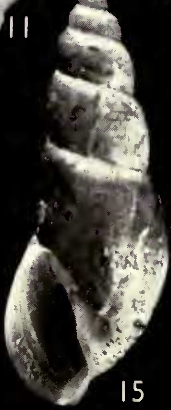
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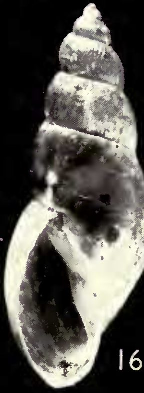
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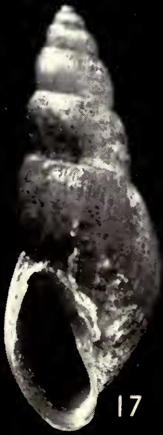
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PLATE 8

Figs. 1–6. *Bulinus forskali*, laboratory bred from a stock originating from Lagoa Panguila, Luanda.
Figs. 7, 8. *B. forskali*, Lagoa Lalama, Luanda.
Figs. 9–11. *B. forskali*, Lagoa Cabungabunga, Luanda.
Figs. 12–14. *B. forskali*, Dongo, Cuanza, Sul.
Figs. 15, 16. *B. forskali*, Lagoa Dalagosa, Luanda.
Figs. 17–19. *Burnupia* sp. (c.f. *gordonensis*) Rio Moembege, Cuanza Norte.
Figs. 20–22. *Burnupia gordonensis*, holotype, B.M. (N.H.) coll. no. 1904.4.29.40.

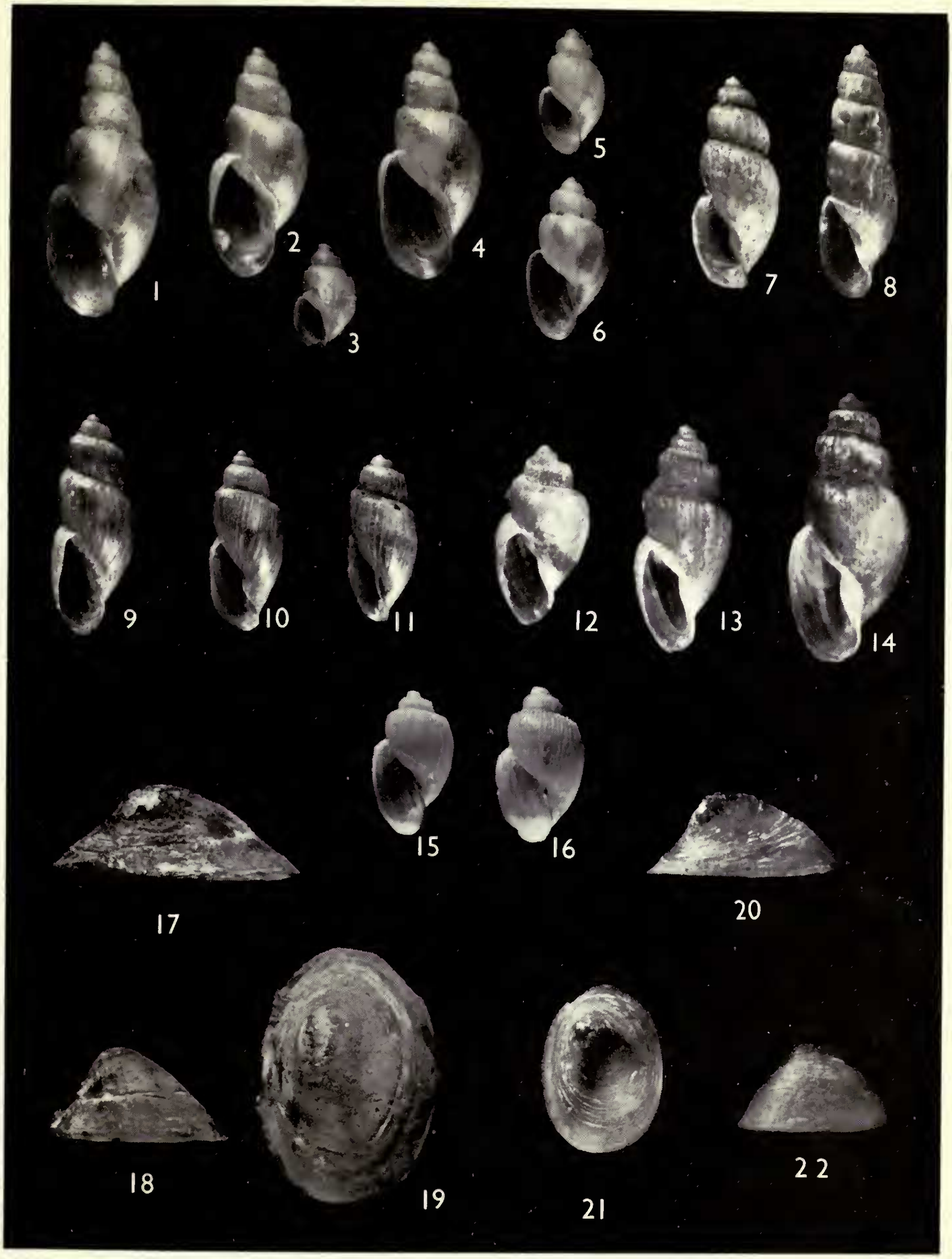
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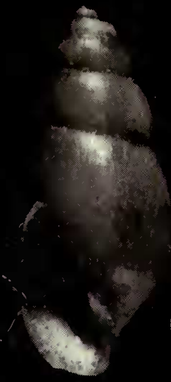
PLATE 9

Bulinus scalaris

FIGS. 1–3. *B. scalaris*, syntypes, Berlin Museum.
FIGS. 4–6. *B. benguelensis*, syntypes, B.M. (N.H.) coll. no. 196280.
FIGS. 7, 8. *B. canescens*, syntypes, B.M. (N.H.) coll. no. 93.2.4.606–7.

PLATE 9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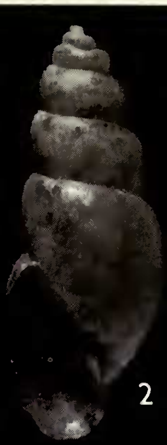
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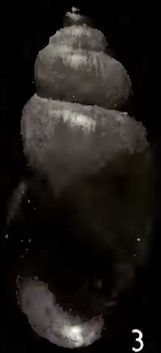
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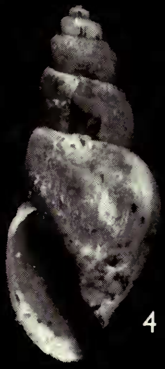
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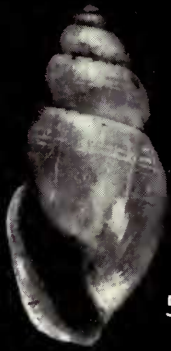
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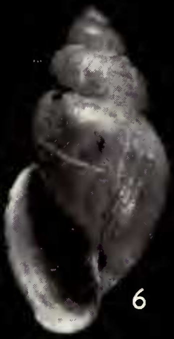
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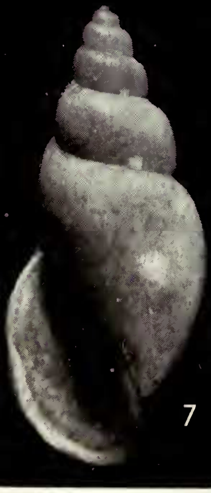
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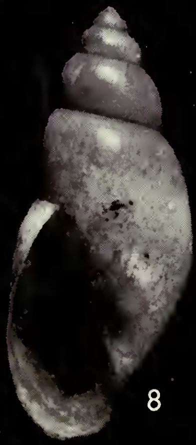
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PLATE 10

Bulinus scalaris, apical whorls of one of the syntypes to show ribbing and carination. (× 50.)

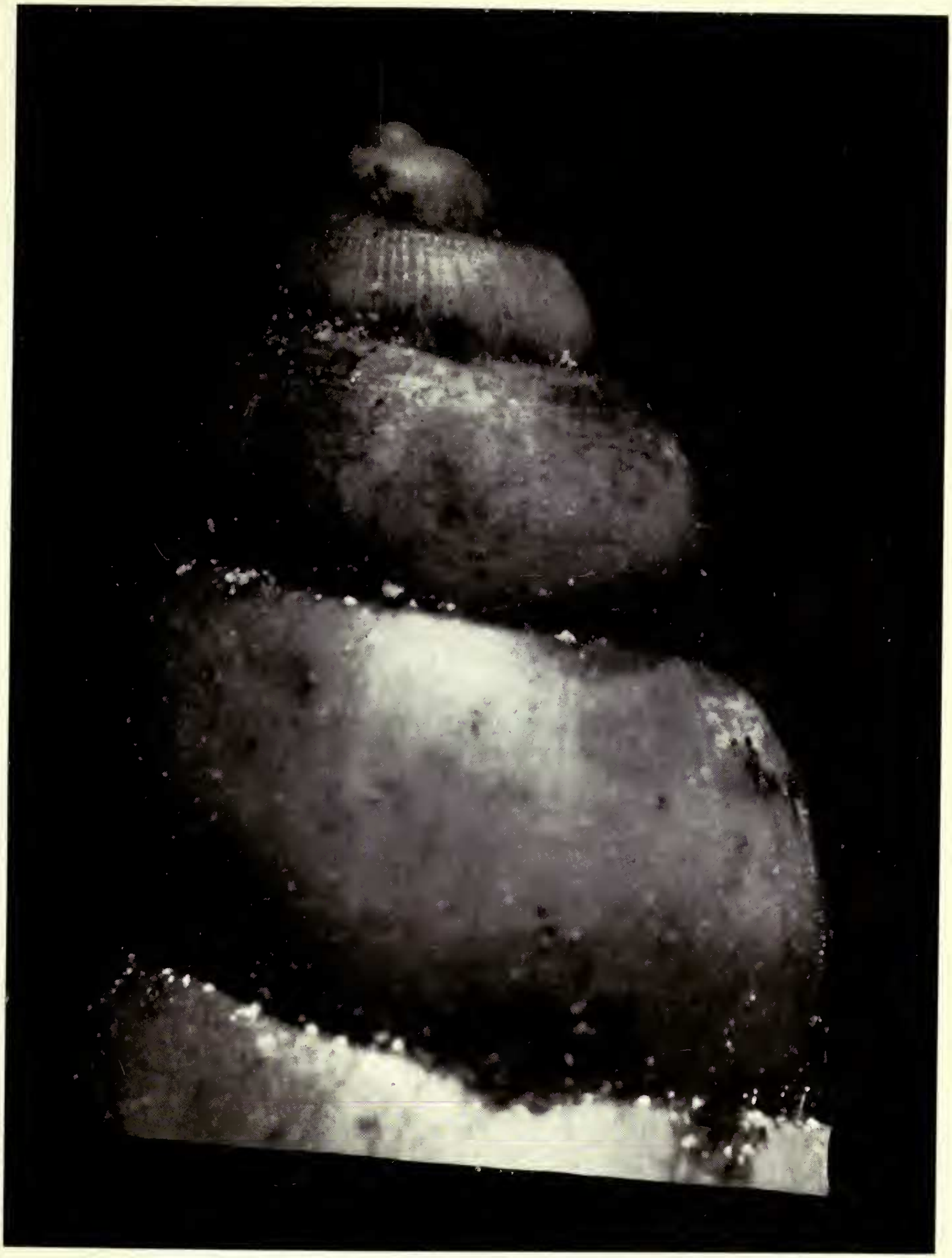

PLATE 11

FIGS. 1–3. *Bulinus crystallinus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.636–8.
FIGS. 4–7. *B. crystallinus*, Salzar, Cuanza Norte.
FIGS. 8–11. *Bulinus truncatus rohlfsi*, Lagoa Cabemba, Luanda.
FIGS. 12–15. *B. truncatus rohlfsi*, Lagoa Panguila, Luanda.
FIGS. 16–19. *B. truncatus rohlfsi*, laboratory bred from stock originating from Lagoa Cabemba.

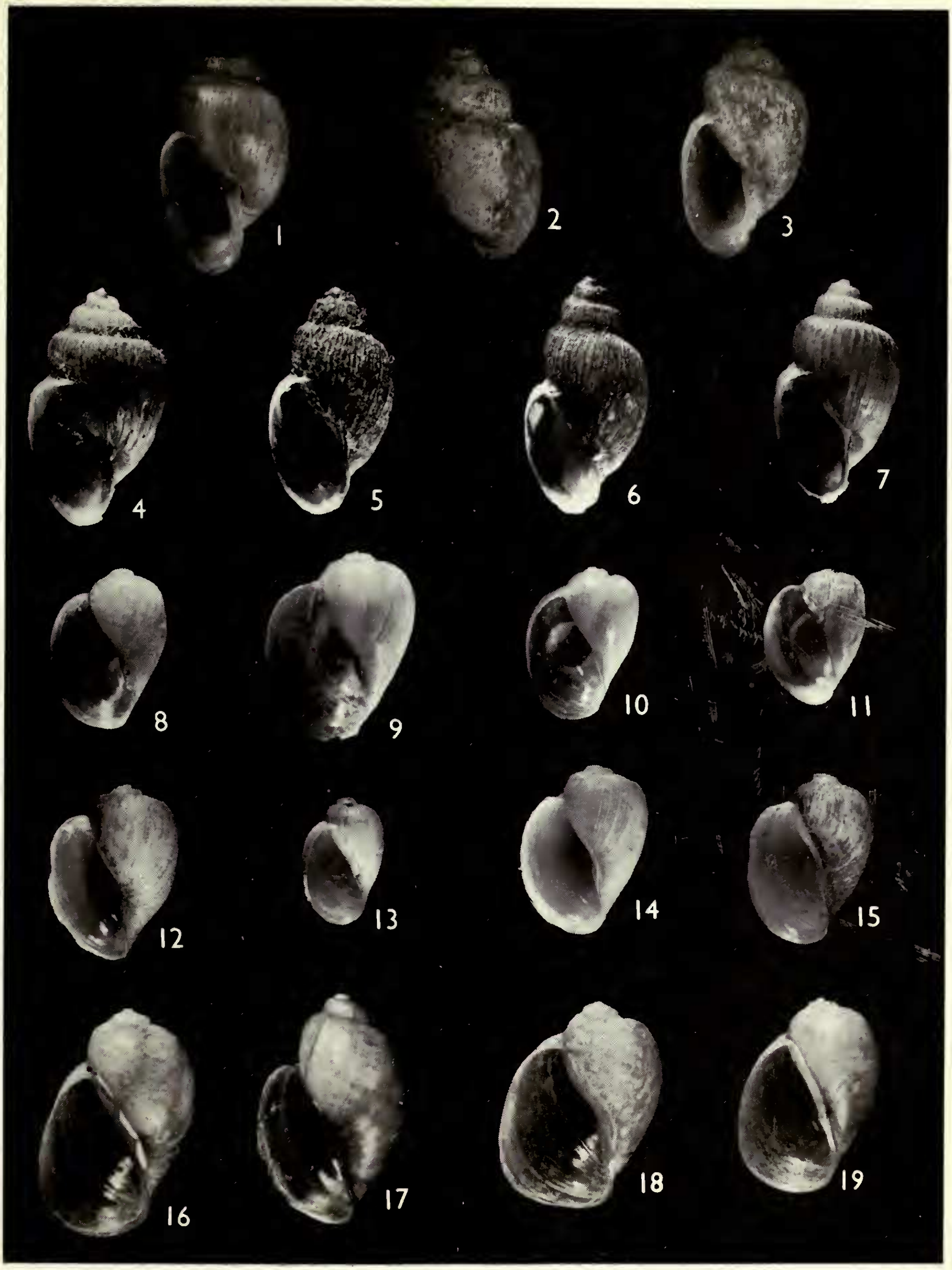
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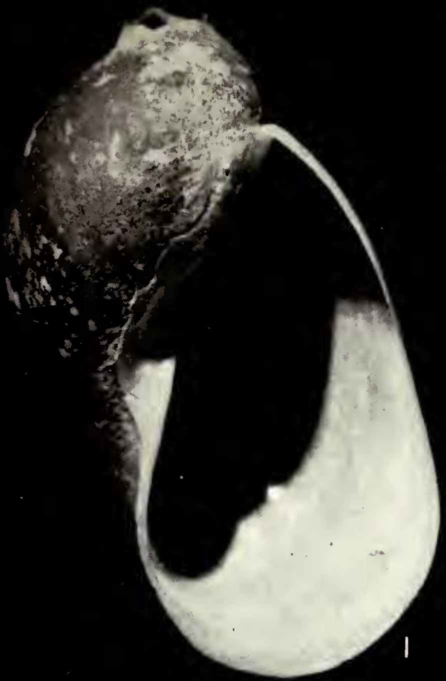
PLATE 12

Lymnaea natalensis.

FIG. 1. *L. bocageana*, syntype, B.M. (N.H.) coll. no. 93.2.4.1341.
FIG. 2. *L. orophila*, syntype, B.M. (N.H.) coll. no. 93.2.4.1344.
FIG. 3. *L. sordulenta*, syntype, B.M. (N.H.) coll. no. 93.2.4.1332.
FIG. 4. *L. succinoides* (= *benguelensis*), syntype, B.M. (N.H.) coll. no. 76.6.8.55.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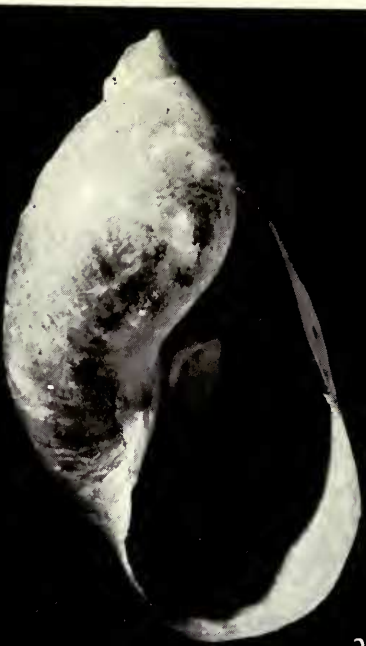
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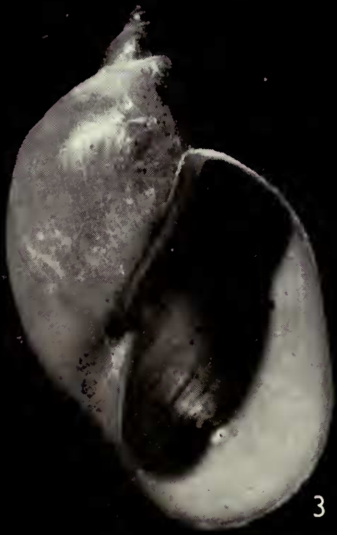
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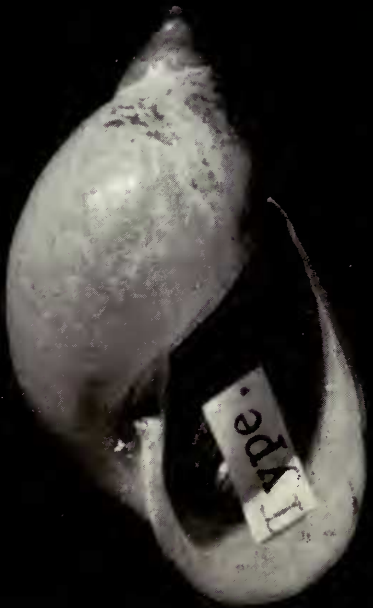

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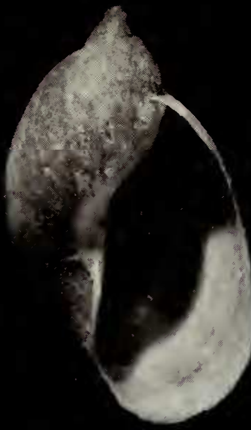
PLATE 13

Lymnaea natalensis.

FIG. 1. *L. natalensis*, Quissol 1, Malange.
FIG. 2. *L. natalensis*, Quissol 2, Malange.
FIG. 3. *L. natalensis*, Lagoa Panguila, Luanda.
FIG. 4. *L. natalensis*, Fazenda Tentativa, Luanda.
FIG. 5. *L. natalensis*, Capemba & San Jose, Huila.
FIG. 6. *L. natalensis*, Cangombe, Huila.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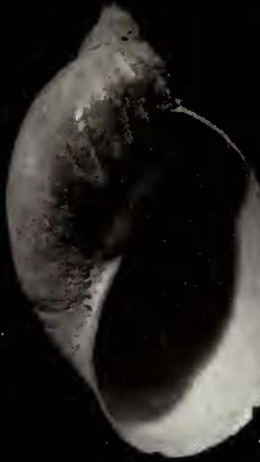
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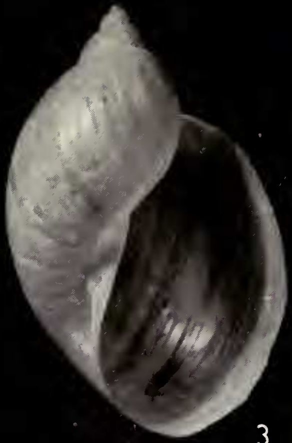
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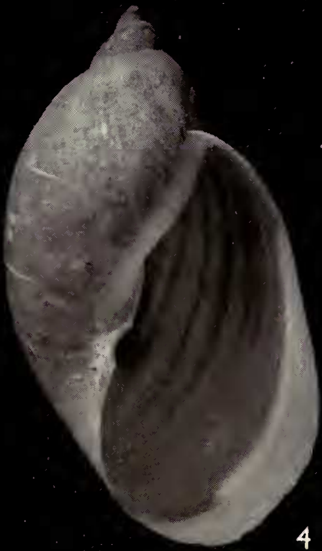
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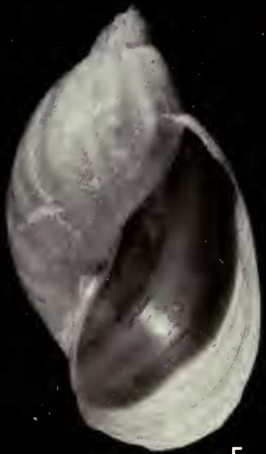
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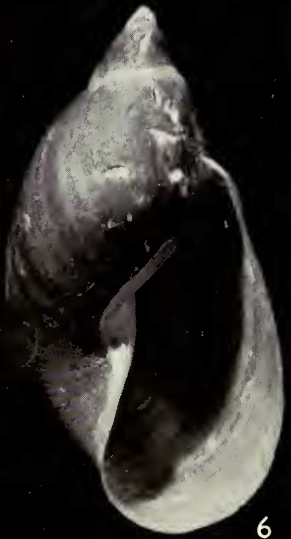
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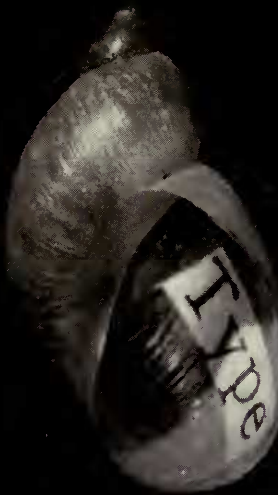
PLATE 14

Figs. 1–3. *Succinea badia*, syntypes, B.M. (N.H.) coll. no. 93.2.4.936–8. (× 5).
Figs. 4, 5. *S. concisa*, syntypes, B.M. (N.H.) coll. no. 93.2.4.950–1.
Fig. 6. *S. patentissima*, Lagoa Lumango, Luanda.
Figs. 7, 8. *Bellamya unicolor*, Rio Cuije, Malange. (× 3).
Fig. 9. *Gabbia kisalensis*, Rio Cuije, Malange.



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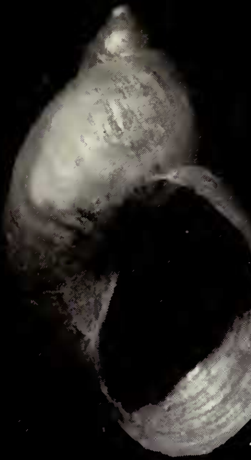

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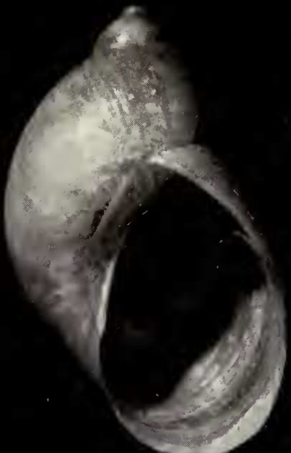

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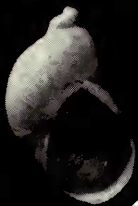

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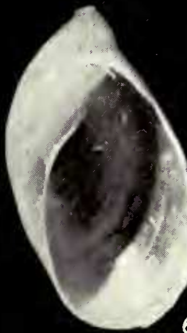

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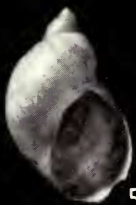

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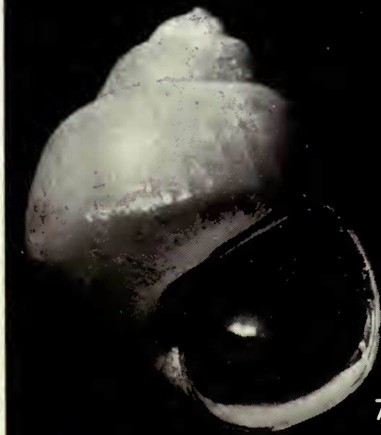

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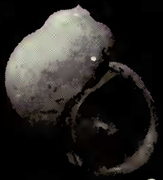

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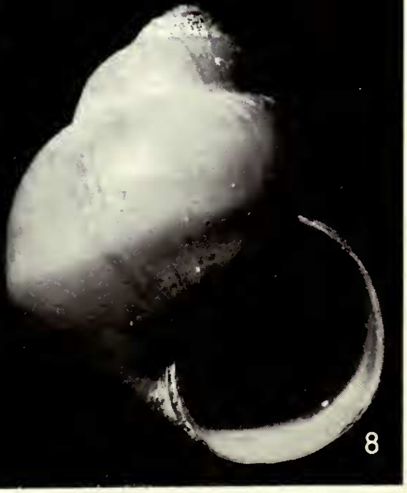

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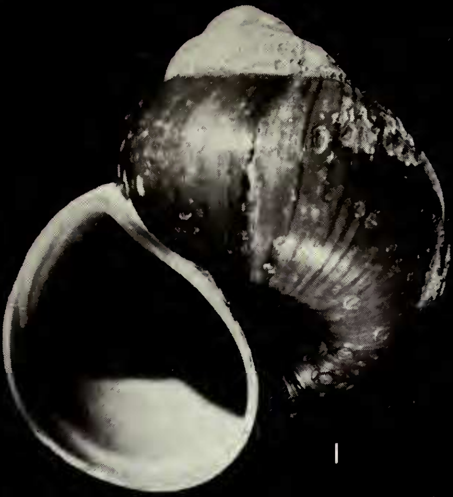
PLATE 15

FIG. 1. *Lanistes ovum*, specimen from the Welwitsch collection, B.M. (N.H.) coll. no. 93.2.4.1821. (× 1·25).

FIG. 2. *L. ovum*, reputed paratype, B.M. (N.H.) coll. no. 196279. (× 1·25).

FIG. 3. *L. libycus*, Rio Lucalla, Malange. (× 2).

FIG. 4. *L. ovum*, Lagoa Matoz, Luanda. (× 1·75).



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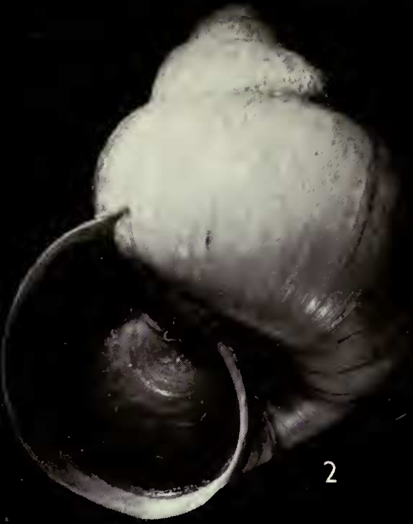

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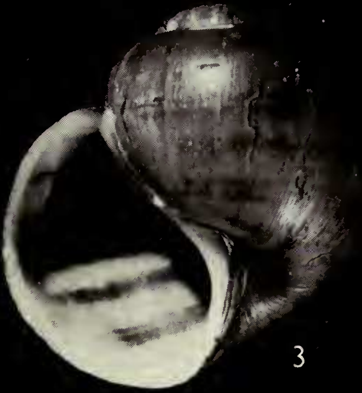

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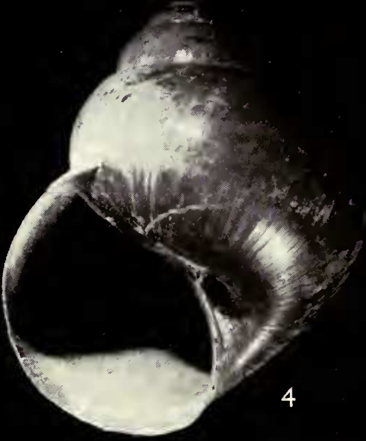

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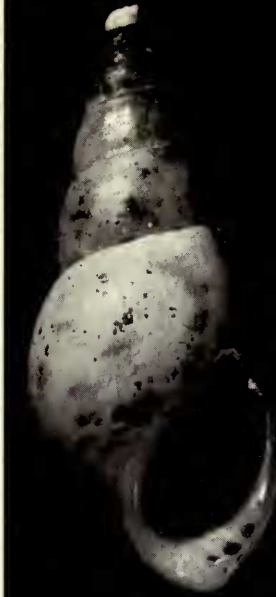
PLATE 16

Fig 1. *Melanoides tuberculata*, Fazenda Tentativa, Luanda.
Fig. 2. *M. tuberculata*, Lagoa Quilunda, Luanda.
Figs. 3, 4. *Cleopatra bulimoides*, Pungo Andongo, Cuanza Norte, B.M. (N.H.) coll. no. 76.6.8.53.
Figs. 5, 6. *Lanistes libycus*, syntypes, B.M. (N.H.) coll. no. 93.2.4.1814–5. (× 2).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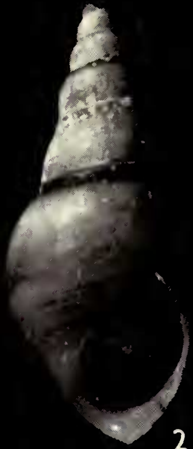
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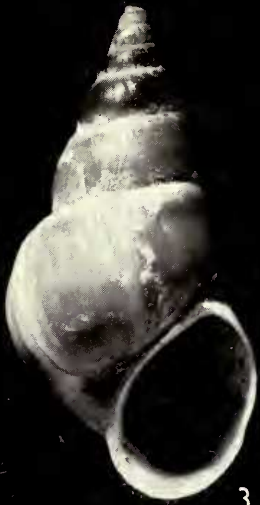
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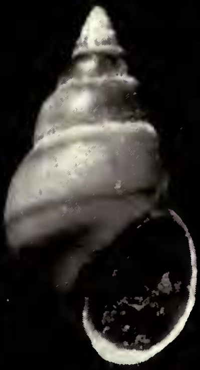
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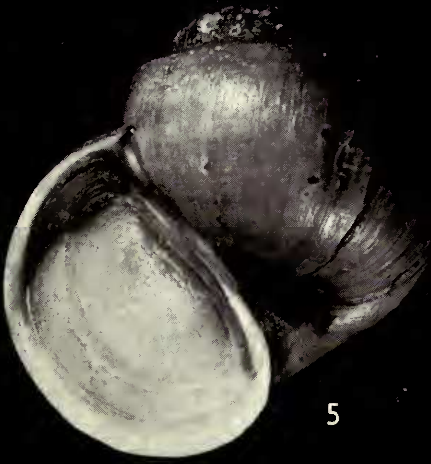
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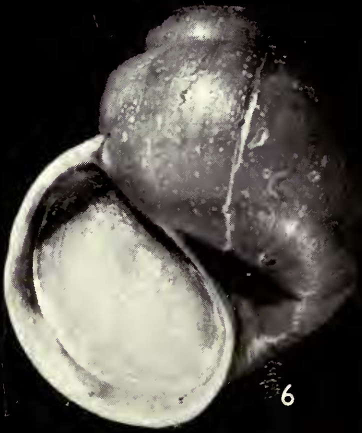
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